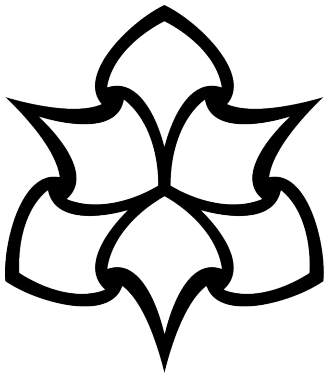

PHYTOGEOGRAPHY AND THE STOICHIOMETRIC NICHE: EXPLORING THEIR INTERPLAY IN SULAWESI

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For the people of Sulawesi whose goodwill,

cheeriness and resourcefulness are the foundation of this thesis.

They deserve far more than tragedy.

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Abstract

The Indonesian island of Sulawesi is comprised of a mosaic of soil types including the largest ultramafic outcrops in the tropics (ultramafic soils are macronutrient low and phytotoxic heavy metal rich). The island's ontogeny is also distinctive, whereby it has formed only recently < 2 million years ago via agglomeration from a number of proto-islands. How the island's phytogeography is influenced by the dual impact of edaphic heterogeneity and island ontogeny is unknown. Equally, how the numerous metal elements influence plant-soil interactions scale up to determine phytogeography is not well understood.

I show here that tree communities in Sulawesi are both influenced by dynamics of island formation and edaphic chemistry. I identify the effect of soils upon foliar metal concentrations of tree communities. This manifests as many species existing within a similar/core stoichiometric niche space (defined by leaf metal axes) irrespective of soil chemistry, but on heavy metal rich soils, species also occupy distinctive niche space far from most other members of the community. As such, I find that soil metals drive the differences in niche space occupied by communities rather than plant macronutrients. I also find that species found across both different soil types and regions in Sulawesi tend to occupy a broader stoichiometric niche than those species restricted to a region and or soil type. Conversely, clades that are overrepresented across different soil types and regions do not show greater niche breadth than those overrepresented on a single soil type and or region, indicating that occupying both a conserved and broad niche can promote dispersal.

This work provides evidence for the interacting roles of island ontogeny and edaphic heterogeneity upon biogeography and the interrelationship with the plant stoichiometric niche.

Contents

1. Introduction

Islands, wet tropical forests and ultramafic soils have all proved productive landscapes for the advancement of ecological thought (Whittaker 1960, MacArthur and Wilson 1963, Hubbell 2000, Harrison and Rajakaruna 2011). The Indonesian island of Sulawesi has a combination of all three of the above yet remains from a botanical and ecological standpoint poorly understood. This thesis co-opts this system to shed light on unanswered questions at the little explored interface between biogeography, ecological stoichiometry and niche theory.

1.1. Biogeography of Southeast Asia

Delineation of biotic regions has long been a task undertaken by biogeographers (Whittaker et al. 2013). The Southeast Asian archipelago spanning from peninsular Malaysia to New Guinea is invariably partitioned between both Asian and Australian biotic regions (Simpson 1977). Partitioning has not been consistent between authors, this has become popularly termed the Wallace line debate after pioneering biogeographer Sir Alfred Russell Wallace who, alongside other early zoogeographers, provided simplistic delineations of the region to either Asian or Australian biotic zones i.e. Lydekker apportioned all islands west of New Guinea to Asia whereas Huxley assigned all islands east of Java and Borneo to Australia (Simpson 1977). Regionalisation of the flora is complex with researchers often following the assignment of islands to a transition area known as Wallacea that encompasses Java, Sulawesi and the Lesser Sunda and Maluku island chains (Van Welzen et al. 2011, Fig. 1).

Whereas in the Neotropics there has been a build-up of an ecologically grounded approach to phytogeography (i.e. the distribution of biota analysed within the context of space, abiota and biotic interaction, e.g. Tuomisto et al. 2003, Eiserhardt et al. 2013, Pennington and Lavin 2016), in Southeast Asia it is comparatively lacking (but see Paoli et al. 2006, Culmsee and Leuschner 2013, Yap et al. 2018).

Phytogeography grounded in phylogeny has been undertaken for numerous plant genera including *Acronychia* (Holzmeyer et al. 2015), *Aglaia* (Grudinski et al. 2014), *Artocarpus* (Williams et al. 2017), *Breynia* (van Welzen et al. 2015), *Cinnamonum* (Huang et al. 2016), *Ficus* (Chantarasuwan et al. 2016), *Goniothalamus* (Thomas et al. 2017), *Macaranga, Mallotus* (van Welzen et al. 2014), *Planchonella* (Swenson et al. 2014) and *Tricosanthes* (De Boer et al. 2015). Dispersal has been observed in the above genera from the Asian affiliate islands

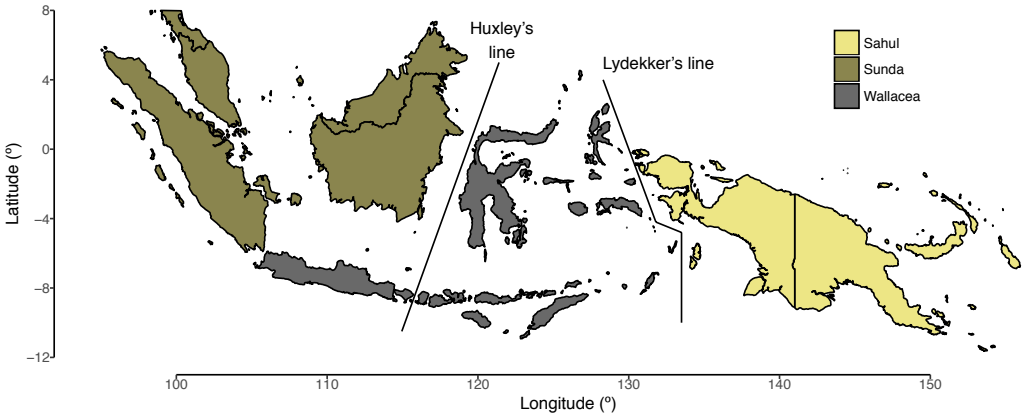


Fig. 1. Map of the Southeast Asian archipelago. Floristic regions following (Van Welzen et al. (2011) and Crayn et al. (2014) are illustrated with colour. Historic biogeographical lines, mentioned in the above text, that were thought to differentiate between Asian and Australian biotas are shown (Simpson 1997). Sulawesi is the island with four peninsulas situated adjacent right of Huxley's line.

Borneo and Sumatra (known as the Sunda region) to Australian affiliated New Guinea (known as Sahul) and vice versa. These events are generally recent, occurring < 12 mya (Crayn et al. 2015). This is concurrent with frequent intra-biome dispersal found previously in the wet tropics (Pennington and Lavin 2016, Dexter et al. 2017) and, as such, the abiotic variables of the archipelago that may limit dispersal and underpin the observed intra-biome regionalisation (Sunda-Wallacea-Sahul) still require attention.

1.2. Sulawesi

1.2.1. Location

Sulawesi is the largest island (182,870 km^2) in the tropical archipelago between Borneo and New Guinea. It is positioned between Borneo and the Moluccas islands. It is K-shaped, made up of four peninsulas, making it unique in being a large island that lacks a substantial interior (Fig. 1).

1.2.2 Floristics and phytogeography

Sulawesi itself is emblematic of the inconclusive biogeographic debate in Southeast Asia. Comprehension of its biota has lacked clarity for both classic (Simpson 1977) and modern study (Holt et al. 2012) when considering biogeographic similarity to islands to its east or west. A position in the amalgamative zone of Wallacea is therefore logical (van Welzen et al. 2011); the most observable phytogeographical discrepancy between Wallacean Sulawesi and Sundaic Borneo to the west is the lack of domination of Dipterocarpaceae in Sulawesi's lowland forest (Raes et al. 2014, Brearley et al. 2016). Botanically, Sulawesi is little studied compared to nearby islands (Kessler et al. 2002, Cannon

2005) with the Lore Lindu highlands in the centre of the island receiving the greatest coverage (Culmsee et al. 2011, Culmsee and Leuschner 2013, Brambach et al. 2017). Baseline knowledge of the flora is growing with the continuation of species discovery (e.g. Girmansyah 2009, Cámara-Leret and Veldkamp 2011, Thomas et al. 2011, Bramley 2012, Low 2013, Brambach et al. 2017) and floristic inventories have been published for a number of locations documenting alluvial (Van Balgooy and Tantra 1986, Pitopang and Ihsan 2014), ultramafic (Van Balgooy and Tantra 1986, Pitopang and Ihsan 2014, Powling et al. 2016), limestone (Van Balgooy and Tantra 1986, Pitopang and Ihsan 2014), riverine (Van Balgooy and Tantra 1986, Erif and Djohan 2013), montane (Milliken and Proctor 1999) and mangrove (Tarigan 2010, Suhardjono 2012) forest communities. Forest plot coverage however is still limited (Brearley et al. in review). Concurrently, intra-island phytogeographical comparison is restricted to studies from the Lore Lindu uplands where most plots are located – this is clearly a challenge when attempting to make a generalisation for the tree flora of Sulawesi as a whole. Historic work by Lam (1945) and Van Balgooy (1987) corroborated migration tracks for the flora from a number of the surrounding islands (i.e. the islands of origin for the migrant taxa that historically colonised Sulawesi), with clear observation of a relative lack of dispersal between Borneo and Sulawesi. Van Balgooy (1987) also carried out a number of regionalisation analyses that, in general, associated Sulawesi most closely with the Philippines and islands to the east (Mollucas, Lesser Sunda Islands and New Guinea).

1.2.3. Zoogeography

Fauna based biogeography has comparatively received 'ample attention' (Lam 1945) both historically (Simpson 1977) and within the context of modern phylogeny grounded biogeography. Work on both monkeys and toads illustrate seven regions of endemism that represent the centre of the island, the eastern, south and southeastern arms and three distinct regions of the northern arm (Evans et al. 2003), findings corroborated across many taxa (Evans et al. 2008, Shekelle et al. 2010, Setiadi et al. 2011). Unsurprisingly, there are taxa that do not adhere precisely to this distribution (Campbell et al. 2007, Von Rintelen et al. 2014, Driller et al. 2015). For instance, the shrew *Crocidura elongata* shows greater genetic divergence between populations within the central region of endemism compared to between populations in central, southeast and eastern Sulawesi (Eldridge et al. 2018). Despite the nuanced difference dependent upon study taxa, the overarching pattern of spatially defined endemism is coherent across the canon of work.

1.3. Geology, soil and climate in Sulawesi

1.3.1. Island formation

The distribution of biota within Sulawesi is undoubtedly linked to the island's geology (Frantz et al. 2018). Historic depiction of island formation suggested an amalgamation of separate islands rafted from surrounding continental areas. The southern peninsula was a Bornean fragment; the northern peninsula had a Philippine origin; and the eastern peninsulas were derived from Australia (Stelbrink et al. 2012). However, very recent collation of data in the most

comprehensive geological assessment of Sulawesi to date has considerably altered the island formation dynamics now envisaged (Nugraha and Hall 2018). Biogeographical analyses mentioned in section 1.2. use the previous conceptualisation of the geological history of Sulawesi; with the collation of new data, Sulawesi's formation has been re-interpreted (Nugraha and Hall 2018) and, as such, studies on biogeography addressing questions within this new geological context are minimal.

Current theory depicts dual rapidity of both terrestrial uplift and basin subsidence where separate proto-islands emerged and have only recently agglomerated (< 2 mya) to form modern Sulawesi (Nugraha and Hall 2018). This is a product of plate extension following post-subduction slab rollback in both the Banda region and Celebes Sea (Nugraha and Hall 2018), put more simply, the uplift of Sulawesi is caused by a spreading/thinning crust (extension) due to the upper plate at subduction zones stretching to fill gaps formed by the descending plate (post-subduction slab rollback). The biogeographical legacy of this recent uplift is unknown and species distribution in such a conspicuous geological system lacks exploration (Frantz et al. 2018).

The three study locations in this thesis have three distinct histories of ontogeny. Morowali is part of a long emergent proto-island (> 20 mya) at the centre of Sulawesi. Wawonii is an island just of the coast of present-day Sulawesi. It emerged only c. 3 mya. Banggai is a product of an even more recent uplift event c. 2 mya but, unlike Wawonii, Banggai is part of now agglomerate mainland Sulawesi.

1.3.2. The edaphic mosaic

Uplifted geologies in Sulawesi include extensive limestone and ultramafic outcrops which are intermixed with a suite of substrates that are poorly defined (Cannon 2005). This forms a mosaic of soil types, the impact of which, upon biota, lacks empirical definition. Although there have been a number of inventories over these various soil types, other than the use of edaphic data within the Lore Lindu studies (Culmsee and Leuschner 2013, Brambach et al. 2017), there has not been an attempt to understand the impact of edaphic heterogeneity on tree communities in Sulawesi. Edaphic drivers of biotic distribution have been regularly identified and the impact of edaphic fertility gradients upon tropical forests is observed in a number of contexts, for example a lack of nitrogen in white sand forests (Quesada et al. 2009, Brearley et al. 2011, Fine and Kembel 2011) and via macronutrient heterogeneity in an alluvial, sandstone and granite system in Borneo (Paoli et al. 2006). Parallels across more complex mosaics such as in Sulawesi is, as yet, unassessed.

1.3.3. Climate

Sulawesi is a predominantly wet tropical island with relatively consistent temperature (Metzger et al. 2013). In general, most areas experience a drier season with less than 100 mm of rain. The areas on the eastern peninsulas in this study experience a ‘dry’ season for less than three months (Whitten and Henderson 2012).

1.4. Ultramafic environments

1.4.1. Ecology

Sulawesi features the largest (c. 15400 km^2) ultramafic outcrop in the tropics (van der Ent et al. 2013 Fig. 2). Ultramafic soil is characterised by potentially phytotoxic heavy metals (e.g. magnesium, nickel, cobalt, chromium), essential nutrient deficiency (e.g. nitrogen, phosphorus, potassium) and low calcium:magnesium ratios (Proctor 2003, Kazakou et al. 2008). The often patchy occurrence of ultramafic outcrops (also known as serpentine in the ecological literature) have been a backdrop for grounding spatial ecological theory in natural history. For instance, the observation of greater extinction in more isolated ultramafic patches and greater colonisation in less isolated patches (Harrison et al. 2001) is confounded by re-emergence of taxa from dormant seed banks (Harrison 2017).

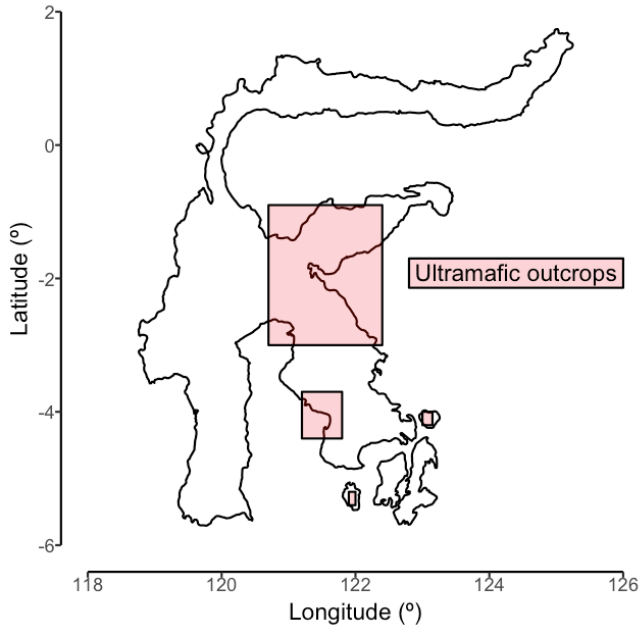


Fig. 2. Ultramafic outcrops in Sulawesi. Adapted from Van der Ent et al. (2015).

Ultramafic environments have provided insight at the crossover between ecology and evolution. Highlighting lineage radiations (Pillon et al. 2009, 2014), pre-adaptation of lineages that undergo edaphic niche shifts (Anacker and Harrison 2012, Cacho and Strauss 2014) and population genetic divergence related to adaptation to metal toxicity (Bratteler et al. 2006, Turner et al. 2010, Hanikenne et al. 2013, Sobczyk et al. 2017). Plant characteristics, or traits, of ultramafic floras have been shown to underlie the differences with surrounding more fertile habitat (Fernandez-Going et al. 2013). Ultramafic plant trait suites are characteristic of stressful environments with stunted plants, low specific leaf area and high C:N ratios (Fernandez-Going et al. 2013). Whilst an assessment of plant traits globally is increasing in momentum (e.g. Díaz et al. 2016), assessment of plants traits in ultramafic environments, and particularly, tropical forests is lacking (but see Hidaka and Kitayama 2009).

1.4.2. Metal accumulation

Ultramafic soil high heavy metal concentrations are a stressor beyond the limitations imposed by classically harsh environments. Heavy metal toxicity operates via numerous mechanisms including impeding photosystem function, auxin transport and inhibiting uptake of other functionally crucial elements (Andresen et al. 2018). To combat this, plants not only exhibit metal exclusion but also toleration and accumulatory and hyper-accumulatory strategies. A hyperaccumulator is defined as a plant containing metal two to three orders of magnitude higher than in leaves of most species on ‘normal’ soils, and at least one order of magnitude greater than the usual range found in plants from

metalliferous soils (Pollard et al. 2014). Metal is present throughout tissues in these taxa, attached to various ligands and transported between cells via both generalist and metal specific membrane transporters (Andresen et al. 2018). Remarkably high concentrations (e.g. 20 % or more) are often found in stem tissue and leaf phloem, epidermis and spongy mesophyll (van der Ent et al. 2017). These taxa in some ultramafic environments can form a significant component of the flora (Reeves et al. 1999). The physiological and competitive advantages of accumulation and hyper-accumulation include herbivore and pathogen defence and allelopathy whereby decomposition of shed leaves produces localised areas of soil toxic to competitors (Boyd 2004). The phylogenetic component of hyper-accumulation is well documented, with most instances restricted to certain clades e.g. Brassicaceae and Phyllanthaceae (Reeves et al. 2018); whether these patterns hold up within the context of wet tropical forest diversity is not certain. A number of tropical tree taxa have been documented to hyperaccumulate, however the first widespread field-based surveys like that performed for macronutrients (Fyllas et al. 2009, Asner et al. 2014) of the metal excluder – tolerator – accumulator - hyper-accumulator continuum across tropical forest communities are only now beginning to be published (van der Ent et al 2018).

1.5. Dispersal disequilibrium

Significant environmental change can be both rapid and incremental i.e. volcanic eruption vs. continual changing climate. Both types of environmental change can lead to novel areas of suitability or unsuitability for species persistence. Due to the temporal limitations of life history traits, species do not instantly disperse to

suitable novel habitat or disappear from newly unsuitable occupied habitat. This leads to a lag in time until species are in equilibrium with their environment. This concept is termed dispersal disequilibrium (Svenning et al. 2015). In recently emergent Amazonian environments, there is no endemism in the recent emergent peatland forests but far greater endemism in the older white sand forests (Table 1). Whether dispersal disequilibrium could persist in a system where a number of proto-islands have merged to form a single island within the last 2 million years, such as in Sulawesi, is not clear.

1.6. Comprehending biota in biogeography

1.6.1. Species

Taxonomic identity, particularly at the species level, has proved a useful baseline unit for biogeography (e.g. MacArthur and Wilson 1963). A number of the studies mentioned in 1.1. are based upon species in the context of regionalisation analyses. Additionally, the species or morphospecies (used if accurate assignment to a published species is not possible i.e. *Garcinia* sp. 1) that exist in a location enables quantification of the diversity of that community. Metrics to define both the magnitude (Fisher et al. 1943, Shannon and Weaver 1949, Simpson 1949, Hill 1973) and compositional change (Jaccard 1912, Whittaker 1960) in diversity

Forest Type	**Plot coverage (ha)**	**Endemic species**	**Age formed**	**Refs**
White sand	5.275	114	6 mya	Fine et al 2010, Draper et al 2018
Peatland	12	0	8 kya	Draper et al. 2018

Table 1. Levels of endemism in different geologically recent Amazonian environments.

amongst communities have been developed and used to successfully distinguish those factors that influence the spread of biota in both space (e.g. Qian and Ricklefs 2007) and time (e.g. Hatosy et al. 2013). Tropical forest species diversity has been observed to shift across seasonality, edaphic and elevation gradients (Aiba and Kitayama 1999, Paoli et al. 2006, Neves et al. 2017). Due to the recent uplift and abiotic variability within and across the islands of Southeast Asia, new insights into factors affecting the spread of tropical tree taxa will undoubtedly emerge.

1.6.2. Phylogeny

Diversity measures based upon species do not consider the interrelationships between them, for instance, they treat *Arabidopsis thaliana* as equally different to *Arabidopsis halleri* as to *Arenga pinnata* – this however is clearly not the case. The incorporation of phylogenies into diversity measures has dealt with this problem. These measures incorporate phylogenetic tree branch length between species that exist within communities, thus species that are more closely related have shorter branch length distance separating them compared to those more distantly related. Early iterations focused upon producing evidence to inform conservation decisions (e.g. Faith 1992). Similar metrics were created to assess these phylogenetic patterns in the context of the ecological facets that lead to the assembly of communities (Webb 2000). Original theory proposed that phylogeny could prove a proxy for plant function and therefore competitive interaction whereby more closely related species are functionally more similar and compete more intensely, this with convergent evolution in mind, has been shown to be erroneous (Mayfield and Levine 2010). Despite these shortcomings, the field

of community phylogenetics has still received a startling amount of research effort (Cadotte and Tucker 2017, Miller et al. 2017). The turnover of tropical forest clades is shaped by both climate and soil (Fine and Kembel 2011, Giehl and Jarenkow 2012, Eiserhardt et al. 2013), an assessment of turnover across tropical island and ultramafic communities is yet to take place.

1.6.3. Function and stoichiometry

The use of taxon and phylogenetic data do not provide direct empirical evidence of how the individuals in a community interact with each other and the environment. The characteristics of these individuals, hereby referred to as functional traits, better define the ecophysiological processes that underscore interactions and consequently how the members of a community co-exist (McGill et al. 2006, Swenson and Enquist 2009). Single traits can be studied (e.g. Bahar et al. 2017, Blonder et al. 2017) or an individual's suite of traits can be placed into multivariate space to provide a more holistic quantification of function (Villéger et al. 2008, Blonder et al. 2014). Temporal (Villéger et al. 2011), spatial (e.g. Lamanna et al. 2014) and abiotic heterogeneity (e.g. Liu et al. 2013) have all been observed to drive distinction in the magnitude and position of communities within multidimensional trait space.

The chemical underpinnings of organism function are intuitive. We can generally think of taxa with distinct functional approaches to have distinct chemistry i.e. the carbon differential between trees and herbs or the phosphorus differential between plants and mammalian herbivores due to bone construction (Meunier et al. 2017). Comprehending organisms in terms of their chemical assemblage enables ecologists to work within the framework of stoichiometry

(Elser et al. 2000). The concept of ecological stoichiometry in the context of a chemical link across an ecological interaction has been successfully co-opted to identify relationships across both differential scales (Elser et al. 2010, Zhang et al. 2018) and type of interaction (Bowes et al. 2017, De la Riva et al. 2017, González et al. 2017, Verboom et al. 2017, Abdala-Roberts et al. 2018, Zhao et al. 2018).

Large scale exploration of carbon, nitrogen and phosphorus soil gradients have been undertaken for their impacts upon tropical tree communities (Asner et al. 2014, Turner et al. 2018). The suite of elements required for organism survival is far more complex than this though (Kaspari and Powers 2016) i.e. potassium and calcium have been identified as drivers of tropical tree growth (Baribault et al. 2012). Whilst we can hypothesise that the diversity of metallic elements present in ultramafic soils affects tropical forests, explicit effects upon tree function and subsequently distribution is still not clear (Proctor 2003).

1.6.4. Stoichiometry and niche theory

The niche species occupy is critical to understanding the distribution of biota. Hutchinson depicted the niche as a multidimensional space defined by variables key to the fitness and survival of species (Hutchinson 1957, 1978). This work adheres to this niche concept. The niche can be defined by the traits an organism exhibits (Kraft et al. 2008, 2015). These traits determine survival and fitness when exposed to different environmental variables and competitors (Kunstler et al. 2016, Umaña et al. 2017a) which subsequently underpins observed biogeography (Eiserhardt et al. 2015, Blonder et al. 2018). The fundamental link between the traits of an organism and the myriad elements that enable the traits to persist intuit that a species niche can equally be defined as its chemical suite

(González et al. 2017). Hereby each element that makes up the stoichiometric ratio of an individual (i.e. Al:P:K:Ca:Mg etc Linder 1995, Ågren 2008) can be used as axes to define the niche. How the stoichiometric niche is influenced by abiota, particularly for plants and the totality of their chemical suite (Kaspari and Powers 2016), is little explored and the consequences for biogeography wholly unknown.

1.7. Forest plots

The forest plot approach allows complex and logistically daunting environs such as wet tropical forests to be studied (Baker et al. 2017). This allowed quantification of biomass, carbon storage and numerous ecological questions to be examined (e.g. Fauset et al. 2015, Umaña et al. 2015). For biogeographical analysis, the plot enables quantification of biotic communities and due to the fact that the plot location can be chosen by the researcher in question, it elicits community observation across both spatial and environmental gradients (Oliveira-Filho et al. 2013). This being advantageous comparative to those biogeographical analyses focused only upon narrower clades, which are limited to studying only the abiotic effects of areas occupied by the constituent lineages (Oliveira-Filho et al. 2013).

In this thesis, we examine the forests of Sulawesi within the context of taxon-based diversity, phylogenetics and ecological stoichiometry across a recently established plot series. This is an integrated approach to assess the floristic impact of the island's formation and edaphic mosaic of ultramafic and other soils. Specifically, we examine how the complex of soils affects tree foliar

stoichiometry (12 elements analysed) and identify how this relates to the distribution of species across an island recently formed from a series of proto-islands < 2 mya.

In the first chapter, we look at the interplay of dispersal disequilibrium following island agglomeration and extreme soils to test:

1) Whether island formation and edaphic heterogeneity drives the diversity and distribution of tree species across Sulawesi.

The next two chapters use the advantages of Hutchinson's duality. This is the severing of the multidimensional species niche from the species physical place within the environment (which Hutchinson (1957) termed the biotope), this duality allows us to understand whether or not the niche changes with environment (Colwell and Rangel 2009). We first approach the system found in Sulawesi, from this environment-to-niche angle, to test:

2) If edaphic factors drive the occupied stoichiometric niche.

Hutchinson's duality also allows us to assess how the geographical distribution of species relates to niche differences between species (Colwell and Rangel 2009). We look at this niche-to-environment link to test:

3) If stoichiometric niche position drives dispersal across soils and regions of different ontogeny.

What causes species to become common or rare is a question that continues to intrigue ecologists. Work by Umaña et al. (2015, 2017b) has identified a link between species rarity and distinctiveness in plant function. Specifically, they have observed that being functionally different from most species within a community is a feature of rare species. We follow this framework to test:

4) If species stoichiometric distinctiveness affects species abundance.

In brief, we find that whilst species diversity was invariant across the plot series, there was a large turnover in species composition between plots driven by legacy effects of island ontogeny but also mediated by the stoichiometric niche occupied by species, which interacts with soil chemistry to drive the distribution and abundance of species across Sulawesi.

2. Recent island ontogeny shapes Sulawesi's tropical tree communities.

Summary

This study aims to uncover the impact of island ontogeny, agglomeration and extreme soil heterogeneity upon tropical tree communities. Does diversity correlate positively with region age? Do communities show high species turnover between regions due to legacy effects of being once separated by sea? Or are communities structured by soils, particularly nutrient poor, heavy metal rich ultramafic soils? We use a permanent forest plot series totalling 2.5 ha that covers three regions of Sulawesi, an island formed only recently from multiple proto-islands. The plots sample communities over sand, limestone, mafic and heavy metal rich ultramafic soil. A combination of linear modelling, variance partitioning and NMDS ordination was employed to test the effects of spatial and edaphic distance upon alpha and beta diversity and distribution of oligarchs. Oligarchs being species that dominate tropical wet forest. We find similar alpha diversity across the plot series irrespective of region or soil type. We find a far greater spatial component of beta diversity compared to the edaphic component. Beta diversity between our regions is higher than in the Amazon at similar geographic scales. Spatial rather than edaphic limitation is also found in our analysis of oligarchs. Unlike other harsh tropical environments, we do not observe a clear impact of ultramafic soils on alpha or beta diversity. We identify high beta diversity between regions and a spatial limitation of tree oligarchs. These findings indicate that island ontogeny has left a legacy in tree communities resulting in patterns that differ from the continental tropics.

2.1 Introduction

Research on abiotic drivers of wet tropical tree species diversity has focused on continental areas, while islands are less well studied. It is unclear how strongly tree diversity is influenced by differences in geological history between islands and continents. The timeframe for island formation has been identified to drive the diversification of taxa via direct provision of unoccupied ecological space (Losos and Ricklefs 2009) and indirect provision via new corridors for dispersal to previously inaccessible regions (Moyle et al. 2016, Tänzler et al. 2016). At a community level, the difference between islands that have formed at different points in time is observable, for instance, lowland forests on the island of Borneo are dominated by members of the Dipterocarpaceae whereas adjacent more recently formed islands of Wallacea are not (Brearley et al. 2016). The mechanisms that underpin the magnitude of diversity (alpha diversity), the change in composition (beta diversity) or universal features of diversity such as the species abundance distribution in regions that exhibit rapid geological change, as in the Indonesian Wallacean archipelago, is yet to be explored.

Sulawesi is the largest island in Wallacea and, as such, plays a key role in dispersal between islands (Tänzler et al. 2016). Insights regarding the effect of Sulawesi's abiota upon the distribution of species is, however, sparse. Its current terrestrial landmass is a modern entity uplifted within the last 2 million years; prior to this a number of proto-islands existed with substantial areas between islands inundated with seawater (Nugraha and Hall 2018). The proto-islands of Sulawesi emerged at different points until their recent agglomeration. Earlier emergent proto-islands will have been exposed to a greater number of arriving propagules

from the species source pool in other emerged proto-islands and nearby large landmasses such as Borneo. Exposure to source pools can influence diversity (Pärtel and Zobel 1999). If the areas of Sulawesi that were once earlier emergent proto-islands have accumulated greater diversity is unclear.

Whether dispersal of tree taxa is affected by different histories of inundation and terrestrial formation is unclear. Historical changes in abiotic conditions can have strong legacies in current diversity patterns (Svenning et al. 2015). This manifests as a temporal restraint upon dispersal, with taxa that fail to occupy the entirety of their potential modern range and systems that fail to reach a state of equilibrium (Svenning and Sandel 2013). It has yet to be examined if this phenomenon, termed dispersal disequilibrium, is prevalent when distinct floras form on separate proto-islands and show delayed frequency of dispersal following island agglomeration. The legacy of which would be a lack of floristic homogeneity across regions of separate formative histories.

Soils are key drivers of tropical tree species distribution (Higgins et al. 2011). They impact plant chemistry (Townsend et al. 2008) and growth rate (Zemunik et al. 2018) and lead to differentially adapted communities along edaphic gradients (Turner et al. 2018b). The Sulawesi uplift has deposited a mosaic of soil types that includes those over an extensive outcrop of ultramafic geology. Which is possibly the largest found in the tropics (van der Ent et al. 2013). These soils pose different challenges to plant physiology compared to the better studied infertile white sand and swamp landscapes of the Amazon (Draper et al. 2017, 2019). Ultramafic limitation derives from both a dearth of macronutrients but also a suite of potentially phytotoxic heavy metals. To establish on ultramafic soils,

plants must exhibit a functional strategy to overcome these constraints (Fernandez-Going et al. 2013). If species are unable to establish viable populations on ultramafic soils, then their importance for biogeography shouldn't be understated. Ultramafic outcrops are extensive in archipelagic South-East Asia and occur across the breadth of the island chain (Galey et al. 2017) offering the significant likelihood that if a propagule disperses across this region it will contact these soils. If, in post-agglomeration Sulawesi, dispersal disequilibrium does not predominate we would expect the infertile ultramafic soils to heavily influence the composition and magnitude of diversity.

The effect of different timeframes for terrestrial emergence upon highly ranking taxa along the species abundance distribution, i.e. the taxa that dominate the total number of stems in tropical forests, is not established. Known as oligarchs, these species can obtain large local population sizes spanning entire continental areas of relative abiotic homogeneity. For example *Eschweilera coriacea* (Lecythidaceae) exists from the Andes to the Atlantic coast and can reach relative abundances of > 50 % within communities (ter Steege et al., 2013). These taxa, however, are readily replaced by a new suite of oligarchs along abiotic gradients that favour taxa with a distinct suite of traits (Pitman et al. 2013). Edaphic disparity is no exception to this rule (Arellano et al. 2016). Whether this lack of spatial, but clear edaphic, limitation in oligarchic taxa is upheld across regions that only recently emerged as terrestrial areas such as in Sulawesi is unknown.

To examine the effects of soil and ontogeny upon total tree species diversity and oligarchic taxa we consider two hypotheses.

Hypothesis 1) Tree communities are structured spatially due to dispersal disequilibrium caused by island ontogeny i.e. there is a lack of homogeneity between regions due to the formation of distinct floras in areas of distinct terrestrial formation despite present-day opportunity for overland dispersal.

Prediction 1a) Floristic distinction is observed between study regions despite edaphic similarity between them, resulting in a significant spatial component of beta diversity when accounting for environment. Oligarchies are restricted to each study region but not soil types.

Prediction 1b) Alpha diversity differs between regions due to greater exposure to the source pool in earlier emergent regions and thus more time for colonization and accumulation of greater diversity within those communities.

Hypothesis 2) Tree communities are defined by constraints of soil infertility and heterogeneity. Communities exhibit significant edaphic filtering.

Prediction 2a) Communities are structured by soil type rather than geographical distance, resulting in a significant edaphic component of beta diversity when accounting for geographic distance. Oligarchies are restricted to soil types but not study region.

Prediction 2b) Communities exposed to the extreme infertility of ultramafic soils are comparatively depauperate and comprise of a subset of taxa from surrounding environments as in Amazonian peatland forest (Draper et al. 2017).

To test the above, we utilise data collated from a plot series that covers three regions and four soil types, this being the first dataset to encompass, for wet tropical forest, both such heterogeneity in island ontogeny and extremity in edaphic conditions.

2.2 Materials and Methods

2.2.1 Plot sites, field collections and species composition

Ten lowland 0.25 ha permanent forest plots were established during 2016 (Table A1) following published protocols whereby the diameter of all stems ≥ 10 cm diameter in breast height (dbh; 1.3 m) was measured and the stems permanently tagged (Phillips et al. 2009). Study locations were concentrated on the wet tropical eastern arms of Sulawesi (Metzger et al. 2013). Two plots were located on ultramafic soils in Morowali Nature Reserve at the centre of the Sulawesi mafic/ultramafic ophiolite complex (Fig 1). Plot quadruplets were set up at the eastern and south-eastern periphery of the mafic/ultramafic ophiolite complex. At the eastern periphery, on the Banggai peninsula, the quadruplet

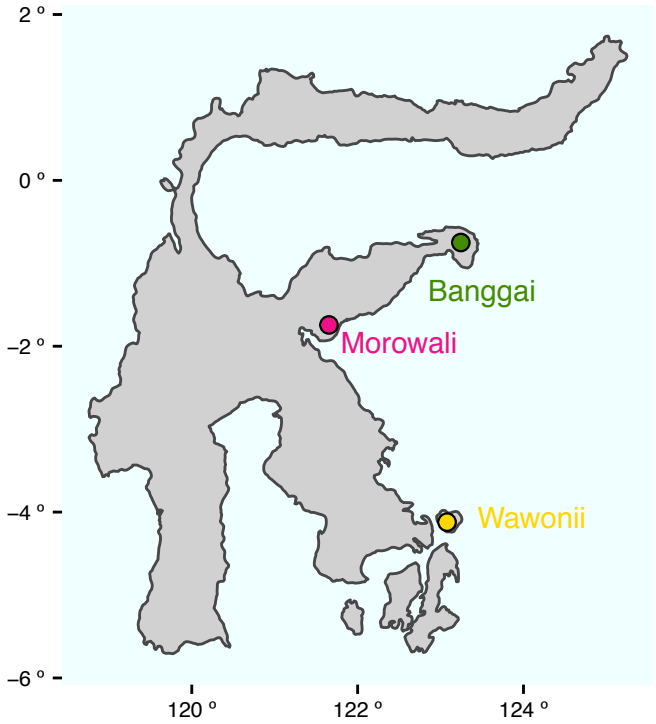


Fig. 1. Map of research localities for permanent forest plots in Sulawesi established in this study. Banggai plots consist of a mafic (2 x) and limestone (2 x) quadruplet. Morowali an ultramafic plot pair and Wawonii an ultramafic (2 x) and sand (2 x) quadruplet.

consisted of two plots on mafic (basalt) soils, a single plot on a limestone hill and another in a limestone valley. At the south-eastern periphery, on Wawonii Island, two plots were located on ultramafic soils and two on sand overlaying ultramafic bedrock. In addition to edaphic heterogeneity between locations, each region has a distinct ontogeny (Nugraha and Hall 2018). Plots on the Banggai peninsula are the most recently emergent, within the last 3 million years, whilst the sites at Morowali and Wawonii are older, emergent within the last 4 million years, yet their ontogeny is clearly distinct with Morowali toward the centre of mainland Sulawesi and Wawonii an island off the south-eastern peninsula.

Herbarium specimens for all taxa were collected and deposited at Herbaria in Kew and Bogor (a set for Palu are currently stored at Bogor). Preliminary field identification used Utteridge & Bramley, (2014). Final identification of collected herbarium specimens was undertaken at Kew. All individuals were assigned to genera with those taxa that did not match currently published species assigned as having an affinity to another species (10 % of stems) or as a morphospecies within the assigned genus (42 %).

Soil samples were collected from each of the 10 x 10 m subplots within each plot and composited to form a single sample per plot. Total C measurement used the Walkley and Black method, total N the Kjeldahl method and total soil Al, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Ni, P and Zn was quantified via digestion of 0.5 g soil in 5 ml HNO_3 and 1 ml $HClO_4$ at 100 to 200 ° C by ramping over a 7 hour period then diluted to 25 ml with deionised water and analysis on an Agilent Technologies 4100 microwave plasma atomic emission spectrometer (Co, Cr and Ni) or an Agilent Technologies 200 Series atomic absorption spectrometer (all other

elements). We reduced soil chemical data to five principal component axes that accounted for > 90 % variability in the full dataset. Axes 1 and 3 accounted for variability in micronutrients and soil trace elements Co, Cr, Cu, Fe, Mn, Ni and Zn, axis 2: Al, C and phytonutrients Ca, N and P, axis 4: Co and Mg, and axis 5: K. Full loadings can be found in the appendix (Table A2).

2.2.2 Alpha diversity

Plot coverage estimates, alpha diversity and interpolated (rarefied) equivalents (representative of the plot with fewest individuals: 105 trees in this study) in terms of Hill number conversions of species richness, Shannon and Simpson diversities was performed with iNext (Chao et al. 2014, Hsieh et al. 2016). The use of Hill numbers overcomes the problems related to the lack of a linear relationship between abundance-weighted diversity measures and increasing species richness when partitioning diversity between assemblages (Chiu et al. 2014). Species richness, Shannon and Simpson diversity equivalents are defined by a weighting parameter q with values 0, 1 and 2 respectively (Hill 1973) and we refer to alpha diversity results within this context. General linear models were used to identify the effect of region and soil axes upon alpha diversity. We also calculated Fisher's alpha diversity for comparison with regional datasets.

2.2.3 Beta diversity

Jaccard (incidence based) and Bray Curtis (abundance weighted) beta diversity measures and their components were calculated for plot pairs. Jaccard components known as nestedness and turnover (Baselga 2010) quantify the degree to which beta diversity between a pair of assemblages is due to either one community being a subset of the other (nestedness) or due to the presence of

species unique to each assemblage (turnover). Bray-Curtis component equivalents were also calculated. Beta diversity measures were calculated in the R package betapart (Baselga 2017) with their components visualised using ternary plots in ggtern (Hamilton 2017). The dissimilarity measures of beta calculated in betapart were converted to similarity measures (1 – dissimilarity) to conform with ternary plot requirement for variables to sum to a constant. Multiple regression models of distance matrices were used to discern effects of spatial and edaphic distance upon pairwise beta diversity measures with permutation testing (999 permutations) to identify significance in the R package ecodist. Edaphic distance is defined as the Euclidean distance in 5-dimensional (5 PCA axes) space between plots. The variance in the model explained by space and edaphic distance and their interaction was quantified with code from (Swenson 2014).

We performed non-metric dimensional scaling (NMDS) ordination on our full tree community dataset and permutation tests (999 permutations) to quantify the significance of soil axes and region upon community composition in the R package vegan.

2.2.4 Oligarchies and rank abundance

We identified oligarchs as defined by (Arellano et al. 2014), these being classified as a species that represent at least 10 % of stems across at least 10 % of plots. The incidence (Jaccard) and abundance weighted (Bray-Curtis) turnover of oligarchs in relation to spatial and edaphic distance was performed as above. To illustrate oligarchic magnitude, we calculated and plotted species rank abundance data across the full plot series, for each region, and for plots edaphically similar across the whole series and subsets of these edaphic groups within regions.

UPGMA cluster analysis was used to delimit groups resulting in three edaphic groups that correspond to the four ultramafic site, five non-ultramafic sites and a single site on a limestone hill.

All analyses were performed in R version 3.4.1 (R Core Team 2017).

2.3 Results

2.3.1 Floristic composition

In total, 1434 trees from 284 taxa were recorded across all ten plots. Burseraceae (140 individuals), Myristicaceae (108), Sapotaceae (108) and Myrtaceae (100) were the most commonly encountered families. *Gironniera subaequalis* (Cannabaceae; 75) and *Castanopsis acuminatissima* (Fagaceae; 48) were the two most common species. Myristicaceae, Myrtaceae and Sapotaceae were the most diverse families with 20, 19 and 18 species respectively. Of the total 285 taxa identified, only seven crossed all three regions, these were *Cerbera odollum* (Apocynaceae), *Endiandra sulavesiana* (Lauraceae), *Garcinia celebica* (Clusiaceae), an unidentified species of *Garcinia*, *Gnetum gnemon* (Gnetaceae) *Myristica koordersii* (Myristicaceae) and an unidentified species of *Syzygium* (Myrtaceae). Five species were present in both Banggai and Morowali, six in both Banggai and Wawonii and 13 in both Morowali and Banggai. A greater number of species (55) were found on more than one soil type.

Extrapolation according to (Hsieh et al. 2016) indicated that our plot size sufficiently covers diversity in our system (Fig. 2).

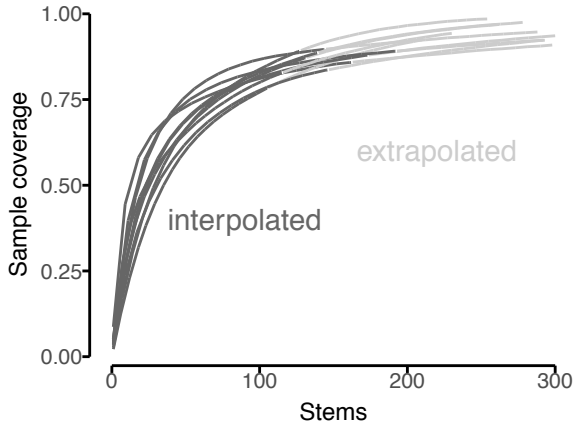


Fig. 2. Estimated sample size coverage across all ten plots in Sulawesi according to Hsieh et al. (2016).

2.3.2 Alpha and beta diversity

A regional impact upon alpha and interpolated alpha diversity metrics under all three weighting parameters was not observed (Fig. 3, Table A3). Soil PCA axes 1, 2 and 5 (Fig. 4) had significant effects on some alpha diversity metrics, these were generally weak (Fig. 5, Table A3). Fisher's alpha ranged from 16 to 34 (Table A1).

Incidence based (Jaccard) and abundance based (Bray Curtis) beta diversity results were consistent across analysis, for simplicity we present Jaccard

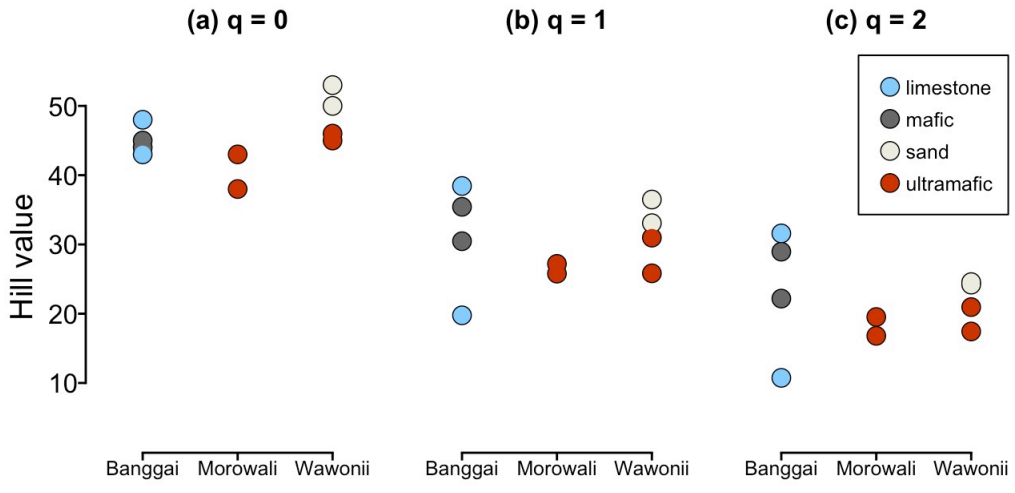


Fig. 3. Abundance unweighted (a) species richness equivalent and abundance weighted (b) Shannon and (c) Simpson diversity equivalent Hill number values across permanent forest plots in three regions of Sulawesi.

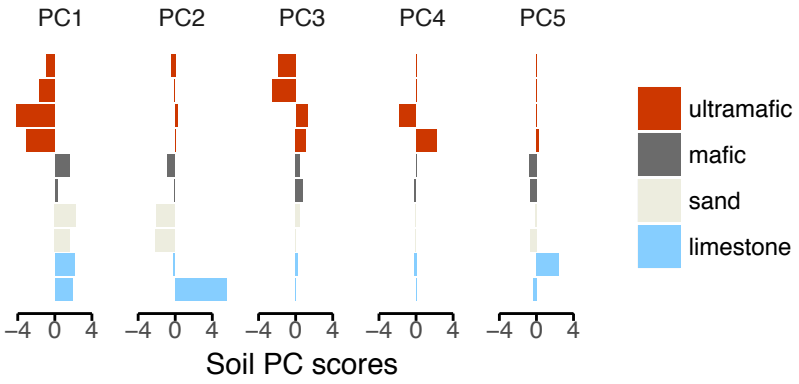


Fig. 4. Edaphic principal component axes scores for all plots in Sulawesi. Colours designate soil types.

dissimilarity results here (Bray Curtis component equivalents can be found in the appendix Fig. A1). Turnover far outweighed nestedness in accounting for Jaccard dissimilarity between all plot pairs (Fig. 6a, b). Both spatial, and to a lesser extent, edaphic distance explained Jaccard dissimilarity results (Adj R^2 = 0.523, spatial p =

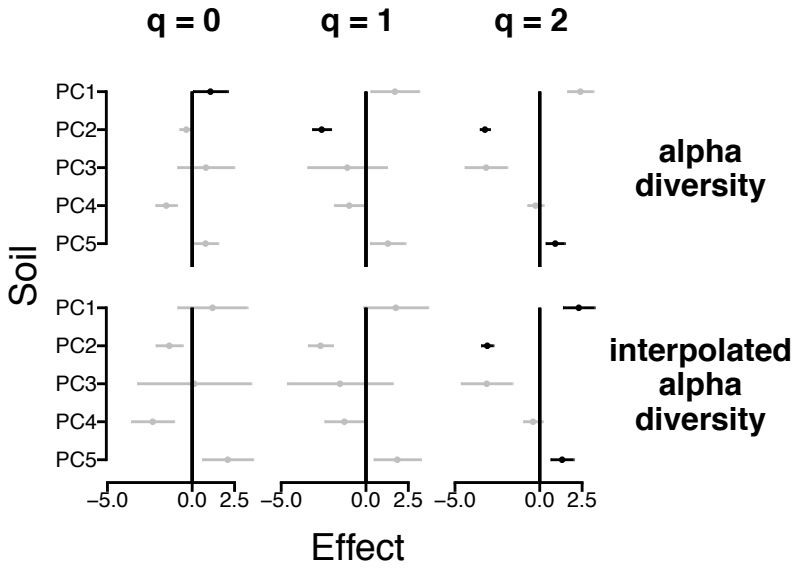


Fig. 5. Effects of edaphic principal components upon, Sulawesi tree community, Hill number alpha and interpolated alpha diversity measures (rows) across an increasing abundance parameter q (columns). q = 0,1,2 are respectively, species richness, Shannon and Simpson diversity equivalent hill numbers. Significant effects ($p < 0.05$) denoted by black symbols. Points represent coefficient estimates and whiskers the standard error for the estimates.

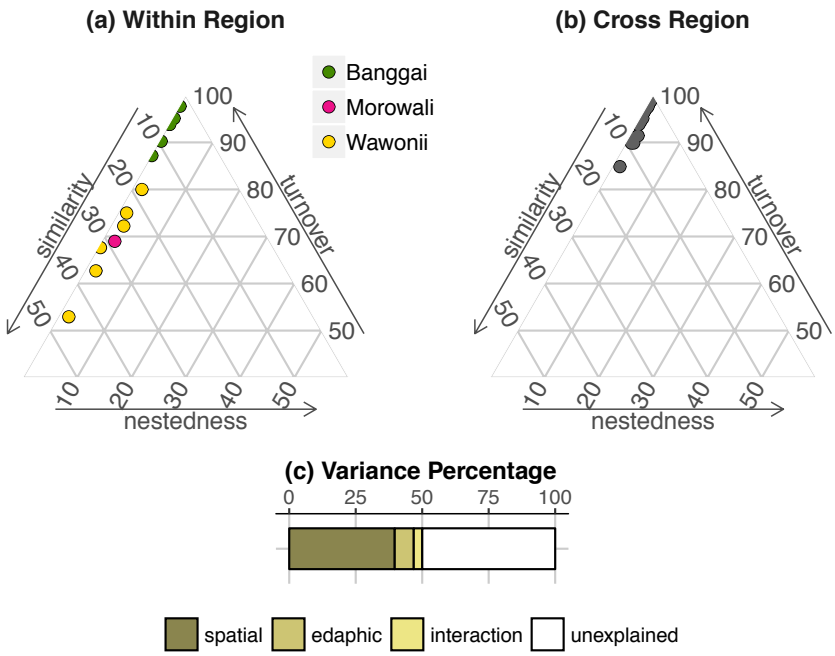


Fig. 6. Ternary plots of the Jaccard similarity measure of beta diversity and the turnover and nestedness components of Jaccard dissimilarity (all displayed as a percentage) across permanent forest plots (a) within and (b) between regions of Sulawesi. (c) Variance in beta diversity explained separately by spatial distance, edaphic distance and their interaction as a percentage of the total variance explained by the combined model.

0.0004, edaphic p = 0.0297, Fig. 6c). This is exemplified by spatial distance accounting for 79 % of the variation, edaphic distance accounting for 14 % and the spatial edaphic interaction accounting for 6 % of the complete model variance. This reflects high beta diversity in plots between regions and relatively reduced beta diversity within regions, although there is still high beta diversity within the Banggai region.

The two NMDS axes (Fig. 7) and permutation tests of effects of environmental variables revealed no impact of soil variables (all axes $p > 0.05$) but a significant impact of the region in which the communities are found ($p = 0.001$).

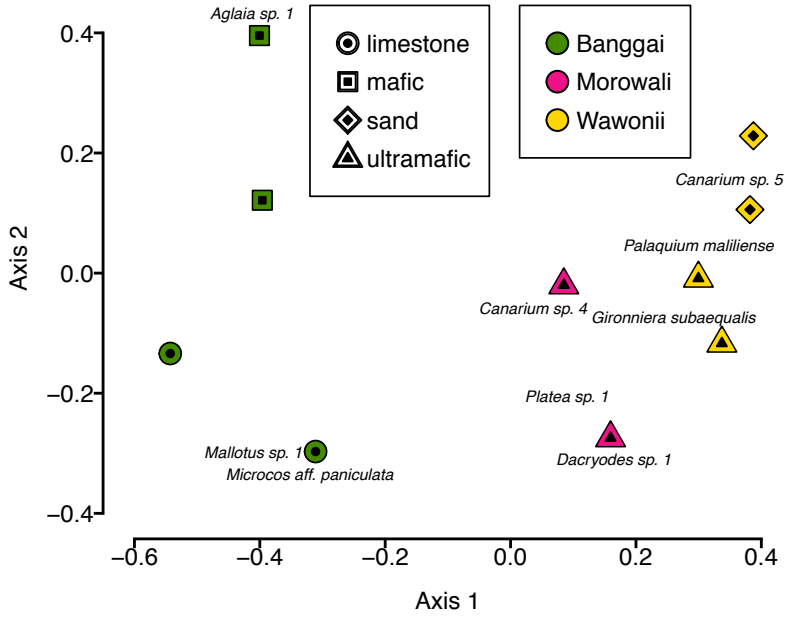


Fig. 7. Ordination of tree communities in Sulawesi forest plots by non-metric multidimensional scaling of abundance weighted tree species composition using Bray Curtis dissimilarity. The significant explanatory effect of region (p = 0.001) is indicated with point colouration. Soil types are denoted by point shape. Oligarchic species position also shown.

2.3.3 Oligarchies and rank abundance

We identify nine oligarchic taxa sensu (Arellano et al. 2014). These being two morphospecies of *Canarium* (Burseraceae), one morphospecies of *Aglaia* (Meliaceae), *Dacryodes* (Burseraceae), *Mallotus* (Euphorbiaceae) and *Platea* (Icacinaceae), *Gironniera subaequalis* (Cannabaceae), *Microcos* aff. *paniculata* (Malvaceae) and *Palaquium maliliense* (Sapotaceae). These species accounted for 10 % of stems in at least one plot and, generally, this frequency was only reached in a single plot for these taxa, most of which were restricted to a particular region. There was no overlap with the seven taxa that cross all three regions.

Linear regression of distance matrices revealed spatial, not edaphic, disparity affected the incidence (Adj R^2 = 0.183, space $p < 0.005$, soil $p > 0.5$) and

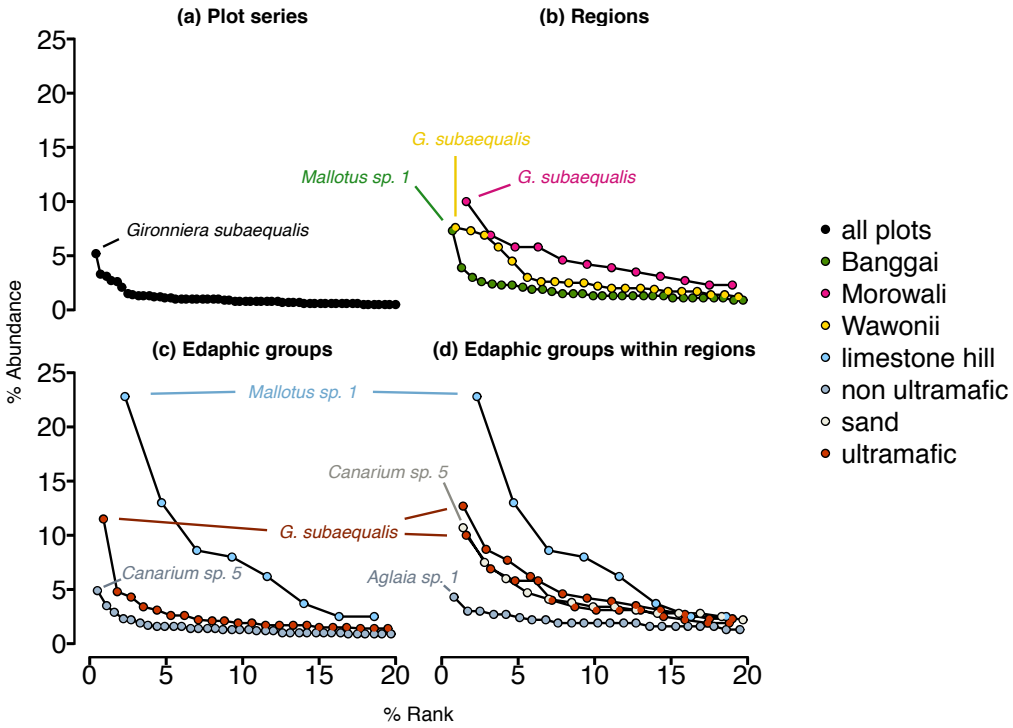


Fig. 8. Tree species percentage rank abundance curves for permanent forest plots in Sulawesi a) all plots b) plots within the same region c) plots on similar soils as defined by UPGMA clustering and d) the regional subsets of those edaphic clusters.

abundance weighted (Adj R^2 = 0.201, space $p < 0.05$, soil $p > 0.05$) beta diversity of these oligarchic taxa across the system. These taxa also clustered regionally in the NMDS plot (Fig. 7). The effect of spatial distance is again clear in relation to rank abundance with only *G. subaequalis* with an abundance of > 5 % across the full plot series, whereas eight species exceed this commonness threshold across plots within each region (Fig. 8a, b). Rank abundance data also highlights the edaphic impact upon commonness, where generally we observe greater abundance amongst common species in plots edaphically similar, particularly those plots edaphically similar and within the same region (Fig. 8c, d).

2.4 Discussion

In support of Hypothesis 1, we find tree communities across Sulawesi exhibit legacy effects of island ontogeny. This manifests in the island's beta diversity where we observed high levels of variance explained by spatial distance but, in opposition to Hypothesis 2, not edaphic distance (Fig. 6c). Although the edaphic component of beta diversity is statistically significant, we do not deem this to be of biological consequence. This is backed up by NMDS permutation results that show a significant effect of region but not edaphic variables. Although these patterns may result from a legacy of island agglomeration we cannot discount that the high spatial turnover observed may be influenced by dispersal capability of the studied taxa (Nekola and White 1999). For instance, Sulawesi's tree flora may be predominantly made up of species lacking traits that support long distance dispersal mechanisms although this seems unlikely in the context of the relatively recent uplift of these islands where life history strategies that promote dispersal will likely have favoured establishment on the proto-islands. Alternate unmeasured environmental factors such as climatic heterogeneity between our three regions could also underpin the pattern we have observed (Franklin et al. 2018), Sulawesi, however, is generally classified as wet tropical (Metzger et al. 2013). Our results contrast starkly with beta diversity in wet tropical Amazonia where at distances of 1400 km between Ecuador and Peru plots generally share 20 % of species (Condit et al. 2002). In Sulawesi, at a considerably smaller scale (200 - 300 km), plots in all cases share less than 15 % of species. Our results are also intriguing when compared to the areas of South-East Asia that once were contiguous but are now separated by seas, specifically the islands of

Borneo and Sumatra and the Malay peninsula. These regions show considerable floristic similarity (Van Welzen, Parnell, & Slik, 2011) whereas in Sulawesi, regions previously separate but now proximate, are in terms of their tree communities, considerably dissimilar.

We observe a lack of nestedness across communities, including plots on ultramafic soils indicative of these communities not being a subset of the surrounding flora, that are able to establish on such extreme substrates. Discordant with Prediction 2b) tree communities on ultramafic soils are distinct and equally as diverse as those surrounding areas, this directly opposes the pattern observed in other habitats deemed stressful for tropical trees (Draper et al. 2017).

Historically, those species that dominate tropical forests, oligarchs, have been thought to not be limited by spatial distance i.e. can dominate across the breadth of the Amazon rain forest. They are clearly, however, limited by environmental heterogeneity, i.e. oligarchs change dramatically across edaphic boundaries (Pitman et al. 2013). We here show that spatial limitation of oligarchs can be induced by legacy effects of island ontogeny. Within Sulawesi, oligarchs do not dominate across regions with different ontogeny. The soils of Sulawesi also impact oligarchy whereby similar soil types have greater proportional abundance of stems apportioned to the few most dominant species. This is exacerbated when looking at these soil types within the regions of distinct ontogeny, again showing the spatial influence of Sulawesi's recent agglomeration upon oligarchs. This provides further evidence for the lack of floristic equilibrium between our three study regions.

The above findings also offer a novel light to look at the phylogenies of taxa across the island of Sulawesi and the ontogenetically similar Philippines. In both these systems, lineages are frequently restricted to particular regions (Merker et al. 2009, Driller et al. 2015, Justiniano et al. 2015, Rowe et al. 2016, Kyriazis et al. 2017, 2018, Eldridge et al. 2018, Frantz et al. 2018, Giarla et al. 2018). These patterns may be linked to dissimilarity primarily due to spatial distance, but one could also place this within the context of dispersal disequilibrium whereby lineages occupy separate proto-islands and then populations/communities fail to establish within newly available suitable habitat on the newly formed agglomerate island.

In conclusion, we have found that extreme edaphic variability has far less of an impact upon both the magnitude and composition of tree species diversity than expected. We observe strong distance decay across both tree communities and oligarchs despite controlling for edaphic variability. The results suggest that island ontogeny, specifically the agglomeration of previously distinct proto-islands, leaves an imprint on the present-day distribution of species. These underlying effects highlight the need for geological data particularly complex island formation dynamics, as found in Sulawesi, to be better integrated within island biogeography and community ecology.

2.5. Appendix

Table A1. Details of permanent forest plots established in Sulawesi.

Longitude	Latitude	Region	Soil type	Stems	Species	Fisher's α
123.12937	-0.65128	Banggai	mafic	127	45	25.9
123.28592	-0.85785	Banggai	limestone/ophiolite	105	48	34.2
123.13108	-0.65017	Banggai	mafic	139	44	22.2
123.28078	-0.86419	Banggai	limestone	162	43	19.1
121.65378	-1.75394	Morowali	ultramafic	115	43	24.9
121.65562	-1.75473	Morowali	ultramafic	144	38	16.8
123.02385	-4.15687	Wawonii	sand	146	53	29.9
123.02515	-4.15616	Wawonii	sand	173	50	23.6
123.04700	-4.15788	Wawonii	ultramafic	131	45	24.2
123.04837	-4.15827	Wawonii	ultramafic	192	46	19.2

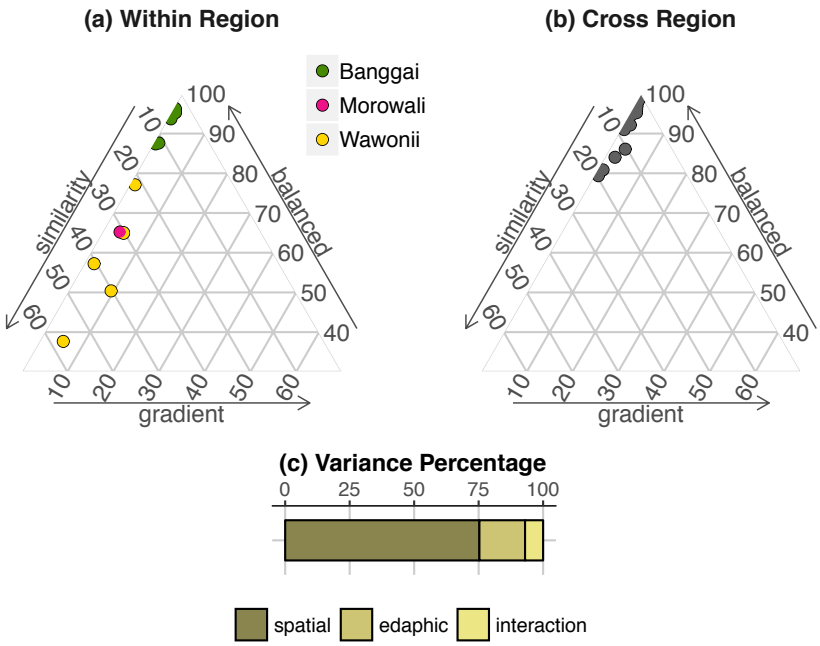
Table A2. Principle component loadings for soil elements quantified in ten forest plots across Sulawesi.

	PC1	PC2	PC3	PC4	PC5
C	-0.043	0.446	-0.166	0.038	0.035
N	-0.044	0.456	-0.052	0.037	0.088
P	0.118	0.446	0.086	0.019	0.018
K	0.189	-0.039	0.038	-0.081	0.941
Ca	0.139	0.436	0.032	-0.003	-0.172
Mg	-0.192	0.030	0.271	0.843	0.126
Fe	-0.409	-0.003	-0.235	0.046	0.035
Al	0.070	0.419	-0.041	-0.049	0.0371
Mn	-0.352	0.073	0.431	0.023	0.062
Cu	-0.346	0.054	-0.324	0.044	0.069
Zn	-0.398	0.098	-0.139	-0.154	0.203
Ni	-0.337	0.012	0.400	-0.076	-0.071
Cr	-0.335	-0.052	-0.472	0.032	0.009
Co	-0.302	0.072	0.369	-0.492	0.029

Table A3. Raw and rarefied alpha diversity statistics with regard to the effect of region and soil axes on alpha diversity in forest plots in Sulawesi. Significance $p < 0.05$ indicated in bold.

						Soil PCA axes														
Metric	**Weighting parameter q**	**Adj R^2**	**Region**			**1**			**2**			**3**			**4**			**5**		
			Df	**F**	**P**	**Df**	**F**	**P**	**df**	**F**	**P**	**df**	**F**	**P**	**df**	**F**	**P**	**df**	**F**	**P**
Hill value	0	0.8	2	4.1	0.20	1	28.8	**0.030**	1	17.0	0.054	1	2.5	0.25	1	8.88	0.10	1	0.13	0.76
Hill value	1	0.8	2	1.0	0.40	1	15.3	0.06	1	39.1	**0.025**	1	1.1	0.39	1	1.21	0.38	1	6.6	0.12
Hill value	2	0.9	2	18.9	**0.05**	1	52.0	**0.020**	1	125.6	**0.008**	1	6.6	0.12	1	0.21	0.69	1	35.2	**0.020**
Rarefied Hill value	0	0.6	2	0.02	0.90	1	4.3	0.17	1	6.3	0.12	1	0.8	0.44	1	4.49	0.17	1	4.6	0.16
Rarefied Hill value	1	0.7	2	1.29	0.40	1	6.8	0.12	1	18.3	0.050	1	1.4	0.35	1	1.11	0.40	1	7.7	0.11
Rarefied Hill value	2	0.9	2	13.7	0.06	1	31.5	**0.03**	1	71.8	**0.013**	1	5.3	**0.002**	1	0.002	0.97	1	33.3	**0.02**

Fig. A1. Ternary plots of the Bray-Curtis similarity measure of beta diversity and the turnover and nestedness components of Bray-Curtis dissimilarity (all displayed as a percentage) across permanent forest plots (a) within and (b) between regions of Sulawesi. (c) Variance in beta diversity explained separately by spatial distance, edaphic distance and their interaction as a percentage of the total variance explained by the combined model.



Bray-Curtis results: Both spatial and to a lesser extent edaphic distance explains Bray-Curtis dissimilarity results (Adj R^2 = 0.489 spatial p = 0.0003, edaphic p = 0.03). This is exemplified by spatial distance accounting for 75 % of the variation explained by the complete model. Edaphic distance accounted for 18 % and spatial/edaphic interaction 7 % of the complete model variance. This reflects high beta diversity in plots between regions and relatively reduced beta diversity within regions although there is still high beta within the Banggai region. Balanced variation in abundance far outweighs abundance gradients where one assemblage is a subset of another in accounting for Bray-Curtis dissimilarity between all plot pairs.

3. Soils induce stoichiometric rarity in tropical trees.

Summary

The interplay between complex soil metal content and tropical tree leaf metal concentrations is not clear. We use a series of 10 x 0.25 ha plots across the edaphic mosaic of Sulawesi including coverage of its metal rich ultramafic areas to directly test how soils impact the tropical tree stoichiometric niche, this is a derivation of the Hutchinsonian niche concept that uses plant metal concentrations as axes of the niche volume. We find that most species exist within core stoichiometric niche space irrespective of soil metal concentrations but there are a minority of species that exist within rare stoichiometric space. These rare species distinguish communities on high heavy metal soils from those on less stressful soil. We find that these rare species are not conserved to particular clades across the plant tree of life. We also show that ultramafic soils vary in their effect upon plants due to heterogeneity in the presence and magnitude of particular soil metals. This causes differentiation in the niche space occupied by species in communities on different ultramafic soil outcrops.

3.1 Introduction

The direct link between a species niche and it's abiotic environment has long been a pillar of ecology (Grinnell 1917). Species' niche quantification varies, with much work having addressed the niche concept in relation to species spatial distribution, abiota and species function (e.g. Elith and Leathwick 2009); the inter-relationship of the niche with ecological stoichiometry has been comparatively less explored (Penuelas et al. 2010, Urbina et al. 2017). Stoichiometry in the context of ecology provides a framework whereby an organism's chemical make-up reflects its function and subsequently its fitness via the fundamental link between cellular level processes reliant upon specific elements that then scale up to determine whole organism function (Meunier et al. 2017). Examples include high investment in P-rich ribosomal RNA that elicits fast growth rates within freshwater systems (Elser et al. 2000); for plants, high foliar P is characteristic of species with short-lived but mechanically delicate leaves that exhibit higher overall growth rates compared to those taxa with long lived and structurally more durable foliage (Wright et al. 2004, Sardans and Peñuelas 2013).

Hutchinson (1957, 1978) crucially removed the concept of a species niche from where it is found within the environment to be a volume within a multivariate space defined by variables that support species persistence. In his often cited 'Concluding Remarks' (1957), Hutchinson provided a graphic depicting a niche volume, one axis of which related to prey size preference of the species in question (Hutchinson 1957). Prey choice as a niche axis has received considerable attention, this includes the relationship between species nutrient requirement and nutrient content of prey (Jackson et al. 2011, Rigolet et al. 2015, Machovsky-

Capuska et al. 2016, Sperfeld et al. 2017). How the broadly comparative relationship between soil and plant chemistry has, particularly for the broad spectrum of elements in plants, received little attention (Kaspari and Powers 2016). This concept of the niche defined by element concentrations can be termed the stoichiometric niche (González et al. 2017) and for plants includes metallic elements accumulated in plants at concentrations that would be toxic for most other species (van der Ent et al. 2013). Multivariate quantification of the stoichiometric niche has so far centred on macronutrients clearly related to organism function i.e. C, N and P. The relationship between the environment and the suite of macronutrients, micronutrients and elements accumulated by plants encapsulating the complexity of the stoichiometric niche remains unresolved.

The relationship between N and P concentrations in soil and the impact upon plant chemistry is well defined (Hidaka and Kitayama 2009, Asner et al. 2014, Turner et al. 2018b). The link between edaphically more complex environments and plant stoichiometry, however, is not. Ultramafic (or serpentine) outcrops form from mantle exposed at either ocean floor spreading centres and subduction zones (Moores 2011). Soils formed over these outcrops exhibit plant limiting chemistry (high heavy metal concentrations: Co, Cr, Ni, low Ca:Mg and P) and have been a system useful for unpicking the ecological basis for the distribution of species (Pillon et al. 2010, Harrison 2017). Ultramafic soils also provides a suitable backdrop for understanding the stoichiometric niche as these regions are where the majority of taxa that hyperaccumulate metal elements are located (van der Ent et al. 2013). The stoichiometric niche position of communities that exist over

ultramafic soils compared to surrounding environments of less complex chemistry is yet to be assessed.

How stoichiometric niche volume changes with the turnover of lineages between communities lacks examination. The process of edaphic filtering favouring lineages that are able to successfully occupy particular soil types is intuitive (Pillon et al. 2010, Cacho and Strauss 2014); these lineages should occupy stoichiometric niche space that most optimises fitness. It is not clear if this manifests as edaphic heterogeneity favouring distinct lineages that, due to phylogenetic niche conservatism along metal tolerance axes, also occupy distinct stoichiometric space from one soil type to another.

How turnover of lineages and the stoichiometric space occupied across communities relates to metal hyperaccumulation is yet to be defined. Hyperaccumulation itself is rare, i.e. only around 700 plant species have been recorded as exhibiting the phenomenon (Reeves et al. 2018). In the tropics, the majority of these are found in the COM (Celestrales, Oxalidales and Malpighiales) clade (Pillon et al. 2010, van der Ent et al. 2018). At a community level, we would expect these rare hyperaccumulator taxa (or other accumulating taxa with high concentrations of metals not reaching threshold formally classifying an hyperaccumulator) on ultramafic soils to occupy very distinct stoichiometric niche space. If these stoichiometrically rare species are restricted to the COM clade in Sulawesi is unknown and whether rarity drives the differentiation in stoichiometric space occupied by communities across soil types is still unclear.

To examine the above, we leverage both the spread of clades and the multivariate stoichiometric niche position of wet tropical forest communities across the Sulawesi edaphic mosaic. The hypotheses we test are below:

Hypothesis 1) Stoichiometric niche placement is primarily driven by soil type.

Prediction 1a) Change in the position within niche space of individuals is related to changes in soil metal axis values and is irrespective of lineage turnover across soil types.

Prediction 1b) Edaphic filters cause individuals within a soil type to occupy a more clustered niche space than to individuals on a different soil type.

Prediction 1c) Soil metal concentrations have a significant impact upon each niche axis (i.e. baseline leaf metal concentrations).

Hypothesis 2) Stoichiometric niche placement is primarily driven by lineage turnover.

Prediction 2) Change in the position within niche space of individuals is related to turnover of lineages between communities and is irrespective of shift in soil metal axis values.

Hypothesis 3) Differences in the niche space occupied by communities is due to outlying individuals on extreme soil types that occupy rare niche space distant from other members of the wider community.

Prediction 3a) High metal concentrations in ultramafic soil chemistry is reflected in those communities by the presence of individuals who occupy rare niche space

as predicted by the fact that a small proportion of plant taxa are able to accumulate metallic elements (Reeves et al. 2018).

Prediction 3b) Species exhibiting stoichiometric rarity are phylogenetically conserved as predicted by the fact that metal accumulation is most often observed within specific clades (Pillon et al. 2010).

3.2 Methods

3.2.1 Sample collection

Samples were collected from the forest plot series outlined in Chapter Two. Two plots are on limestone soils, two on mafic, two on sand and four on ultramafic. The most accessible mature leaves from all species in each plot were collected and dried over fire in the field. Soil samples were taken from the upper 10 cm of topsoil from each 10 x 10 m subplot and amalgamated for further analysis.

3.2.2 Leaf and soil metal data

Seven hundred and twenty-three leaf samples (c. 100 mg) were digested in 10 ml of concentrated nitric acid using a CEM Mars Xpress microwave and made up to 100 ml in ultrapure (18 MΩ) deionised water. Al, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Ni, P and Zn concentrations were quantified using a Thermo-Finnegan iCAP 6300 Duo inductively coupled plasma optical emission spectrometer. Certified reference material (LGC 7162, Strawberry leaves) was analysed alongside the samples, recovery did not differ from reference values for any element (Wilcoxon $P > 0.05$). Similarly, 61 leaf samples were washed by sonicating for five minutes in deionised water; these did not differ from unwashed samples (Wilcoxon $P > 0.05$) so we used unwashed samples for all analyses.

One hundred and one species were sampled multiple times in each plot, the mean metal concentrations for each species within each plot was used for further analysis alongside all species sampled only once per plot. Principal component (PC) analysis of all individual leaves with scaled data (z-scores) indicated that > 90 % of the variation was explained with the inclusion of nine principal component axes - we therefore retain the original scaled data for use in further analysis.

Total soil Al, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Ni, P and Zn was quantified via digestion of 0.5 g soil in 5 ml HNO_3 and 1 ml $HClO_4$ at 100 to 200 ° C by ramping over a 7 hour period then diluted to 25 ml with deionised water and analysed on an Agilent Technologies 4100 microwave plasma atomic emission spectrometer (Co, Cr and Ni) or an Agilent Technologies 200 Series atomic absorption spectrometer (all other elements). We reduced soil metal data to five principal component axes that accounted for > 90 % variability in the full dataset (Table A1).

The complete dataset therefore directly links both complex soil and leaf metal components.

3.2.3 Niche position and rarity

We calculated all distances in Euclidean space between species within plots and between species between plots. These were visualised with violin plots. We then quantified the mean of all the pairwise distances between species both within and between communities (Swenson 2014). We also calculated the standard deviation of the pairwise distances within and between plots to better understand the range of distances between species within and across communities, this reflects the use of standard deviation based metrics in isotopic

niche studies (Layman et al. 2007). The above derivations are equivalent to functional alpha (within plots) and beta (between plots) diversity measures (Swenson 2014).

Stoichiometric rarity was quantified as the mean distance of the individual in stoichiometric space to all other individuals within that community (Violle et al. 2017).

3.2.4 Phylogenetic data

Phylogenetic data was derived from a plant family resolved supertree provided by Gastauer et al. (2017), pruned to consist of the taxa identified across the plot series using Phylomatic (Webb and Donoghue 2005). The resolved phylogeny was then dated according to Magallón et al. (2015). Jaccard-like dissimilarity between plot pairs across the series was calculated (Baselga 2017) with the resulting dissimilarity matrix converted to phylogenetic eigenvectors using forward selection (Blanchet et al. 2008). Selected eigenvectors were retained for further analysis.

3.2.5. Statistical analyses

To test hypotheses one and two, we used linear models (within plots) and permutational analysis of variance tests (between plots) to measure the effect of our five edaphic PC axes and retained phylogenetic eigenvectors upon the mean and standard deviation of pairwise distances between individuals in stoichiometric space. We also performed non metric multidimensional scaling (NMDS) of the mean pairwise distance matrix between communities with permutation tests (999 permutations) to quantify the significance of the five soil PC axes. To further test how soil affected the position of species on niche axes, we modelled leaf metal

concentrations as a function of soil metal concentrations using partial least squares regression (PLS). The PLS approach provides a tool capable of identifying the effects of predictor variables despite covariation with other predictors (Wehrens and Mevik 2007).

To test hypothesis three, we first modelled stoichiometric rarity as a function of edaphic PC axes (fixed effects), region in Sulawesi and identity within different levels of the Linnean hierarchy i.e. order, family, genus, species (random effects). The significance of fixed effects was identified with Type II Wald X^2 tests. Mixed effect model goodness of fit was measured with marginal and conditional R^2 (Nakagawa and Schielzeth 2013). We then tested whether rarity deviates from a random spread across the phylogeny using Blomberg's K (Blomberg et al. 2003) and randomisation tests using phylogenetic independent contrasts (999 permutations). Finally, hierarchical variance partitioning sensu Messier et al. (2010) was used to identify the contributions of order, family, genus and species to variation in stoichiometric rarity.

To account for the skew induced by the outlying stoichiometrically rare taxa we removed the top 10 % rare individuals from the dataset and repeated mean and standard deviation of pairwise distances calculation within and between sites. We also repeated the mixed effects models and phylogenetic signal analysis with the reduced dataset.

All analyses were performed in R version 3.4.1 (R Core Team 2018). The phylogeny was dated with the Bladj algorithm in PhylocomR. Phylogenetic beta diversity calculation and eigenvector selection was performed using betapart and adespatial packages. Differences in niche position within and between plots was

calculated with R code provided by Swenson (2014) for mean pairwise distances which was edited to calculate standard deviation simply by replacing the mean function for a standard deviation function. PLS regression was performed with pls. Rarity was quantified with funrar. The packages lmer4, MuMIn and car were utilised for mixed effect modelling, R^2 and p-value derivation respectively. Phylogenetic signal analysis was performed with phylosignal and variance partitioning used nlme.

3.3 Results

3.3.1 Stoichiometric niche space within and between communities

In general, we find greater mean and standard deviation in pairwise distances in 12-dimensional stoichiometric space (i.e. leaf chemistry) of individuals within communities on ultramafic soils compared to other soil types, the effect disappears however when we remove the top 10 % of stoichiometrically rare individuals from the dataset (Fig. 1a, b). There was a significant effect of two soil PC axes ($p < 0.05$) but no effect of phylogenetic dissimilarity upon within plot mean and standard deviation of pairwise distances (Table A2). The soil axes in question are responsible for variation in metals observed to be accumulated by plants on ultramafic soils but not for the macronutrients Ca, K and P (Fig. 2, Table A3). Thus, for each community we find that the extent of the stoichiometric niche occupied is due to soil chemistry rather than the community's constituent lineages.

When comparing between plots, those plot pairs that consisted of at least a single plot on ultramafic soil had generally larger mean and standard deviation in distance between individuals' in stoichiometric space, the effect disappears however when we remove the top 10 % of stoichiometrically rare individuals from

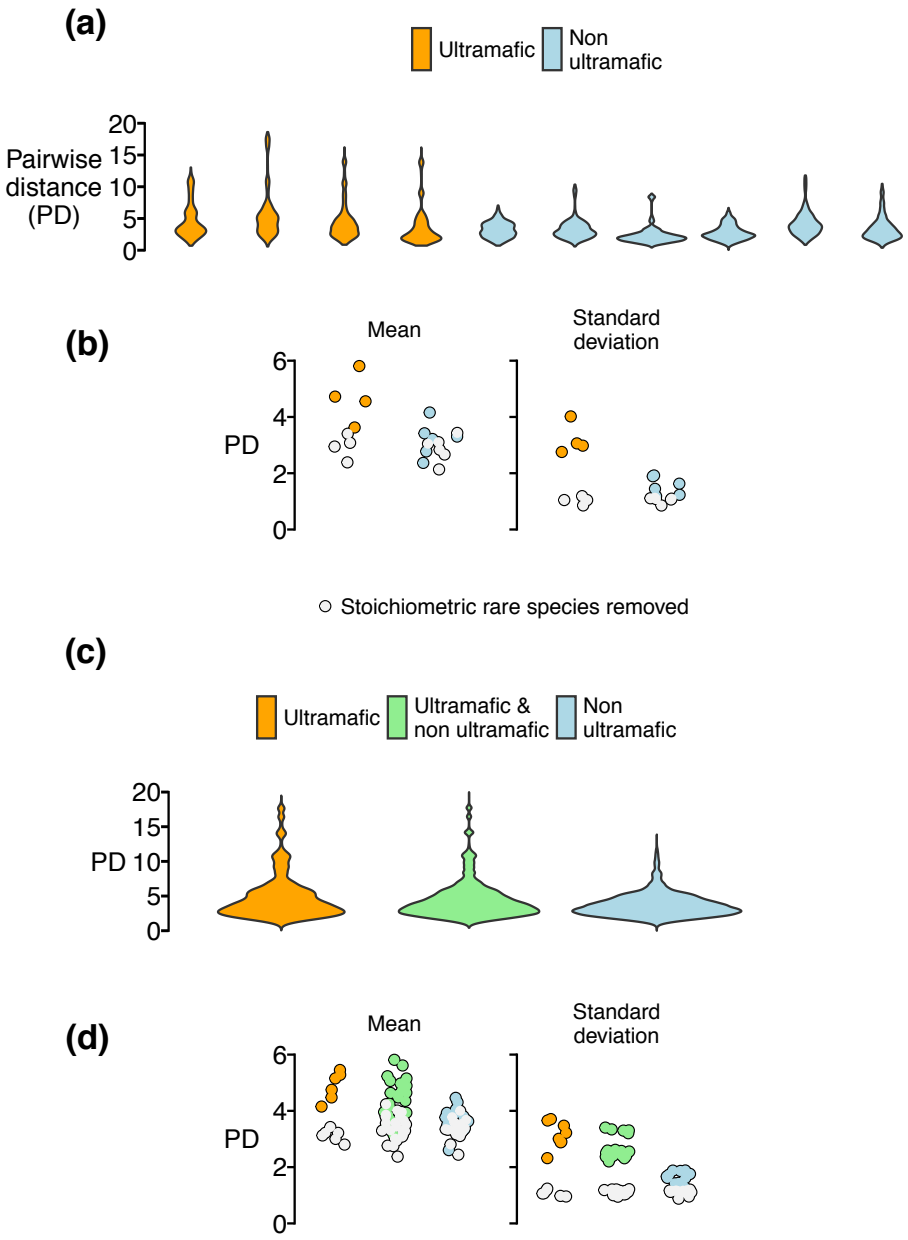


Fig. 1. a) All Euclidean distances between individuals in stoichiometric space in each forest community in Sulawesi and b) the mean and standard deviations of these distances. c) All Euclidean distances between individuals in stoichiometric space between pairs of communities, with distances between individuals in pairs of ultramafic, ultramafic – non-ultramafic and non-ultramafic communities grouped together. d) the mean and standard deviations of the distances between individuals across community pairs. Grey points in c) and d) show mean standard deviation within and between communities when the top 10 % stoichiometrically rare individuals are removed.

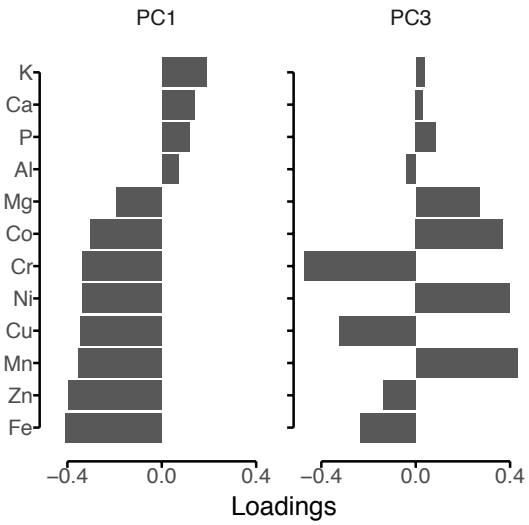


Fig. 2. Loadings of the two soil principal component axes that have a significant effect upon the stoichiometric niche occupied by individuals and communities across the forest communities in Sulawesi.

the dataset (Fig. 1c, d). There was a significant effect of the same soil PC axes (Fig. 2) as for within plot distances, but there was an added effect of phylogenetic dissimilarity upon both mean and

standard deviation in pairwise distance (Table A3) We therefore identify an interplay between both soil heterogeneity and lineage turnover in determining the stoichiometric niche occupied by communities. The two NMDS axes and permutation of environmental variables identify effects of the third soil PC axes ($p < 0.05$, all other PC axes $p > 0.05$, Fig. 3).

We found that the first two PLS axes explained 70 % of the variability in the data. These components represented few large effects (regression coefficient > 0.1 or < -0.1) of soil metal upon leaf metal concentrations (Fig. 4). This is indicative of minimal effects of soil metal heterogeneity upon plant position along stoichiometric niche axes. Large positive effects were however identified for soil Al upon leaf Ca, Cu, and P. Leaf P was negatively affected by soil Cr and positively affected by soil Ca and P. Soil P also had a positive effect upon leaf Ca.

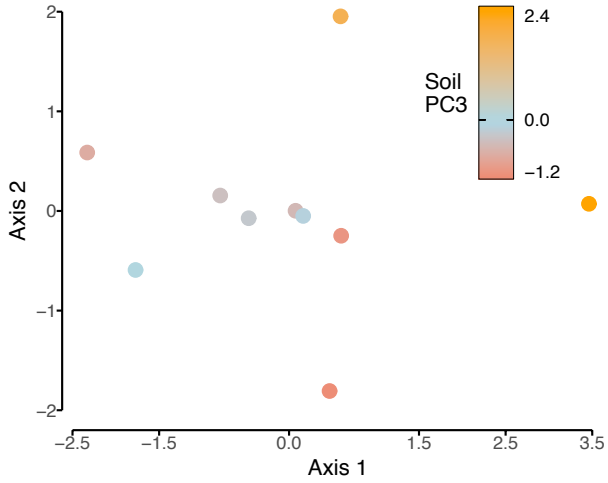


Fig. 3. Non metric multidimensional scaling (NMDS) axes of mean pairwise distance between forest communities in Sulawesi stoichiometric niche space. Colour gradient represents the position of plot sites along the 3rd soil principal component axis. This axis has a significant effect upon stoichiometric distance between communities.

3.3.2 Stoichiometric rarity

The mixed effect model identified a significant effect of the first soil PC axis upon stoichiometric rarity ($\chi^2 = 38$, $p < 0.001$, Fig. 5a, b; marginal and conditional R^2 values were 0.26 and 0.85 respectively). As previously noted, the first soil PC axis accounts for variability in heavy metals and, as such, these metals that are most abundant in ultramafic soils appear to induce stoichiometric rarity. These

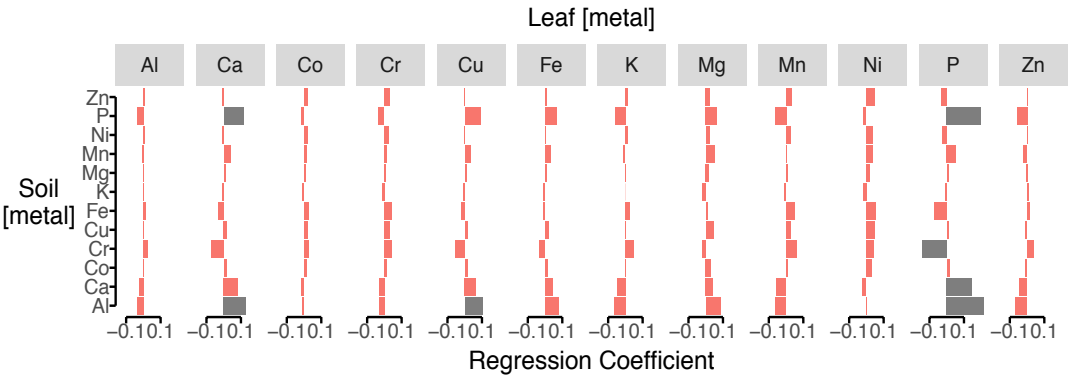


Fig. 4. Regression coefficients of the relationships between soil and leaf metal concentrations in forest communities of Sulawesi derived from the first two components of the partial least squares analysis. Large effects of soil metal upon leaf metal (coefficient > 0.1 or < -0.1) are designated in grey.

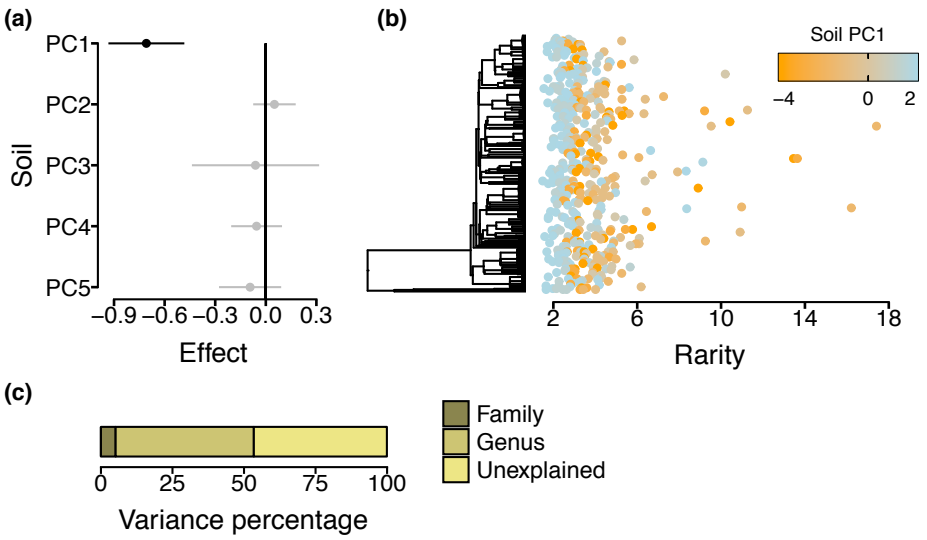


Fig 5. a) Coefficient estimates (effect size and 95 % confidence intervals) from general linear mixed effects models of edaphic principal component (PC) axes upon stoichiometric rarity in forest communities of Sulawesi. Significant effects represented by black symbols. b) Stoichiometric rarity of individuals within the context of phylogeny and edaphic PC1, the only edaphic variable that significantly impacts rarity. c) Results of partitioning variation in stoichiometric rarity across the Linnaean hierarchy, the minimal percentage variation explained by order and species is not displayed.

results were consistent whether or not the top 10 % of rare individuals were included.

A significant deviation from conserved stoichiometric rarity across the phylogeny was observed ($K = 0.19$, $p < 0.05$), however when the top 10 % of stoichiometrically rare species were removed conservation was observed ($K = 0.13$, $p > 0.1$). Variance partitioning indicates 48 % of the variation in stoichiometric rarity was explained by genus (Fig. 5c) but with minimal contributions from order (< 0.01 %), family (5 %) or species (< 0.01 %) (Fig. 6).

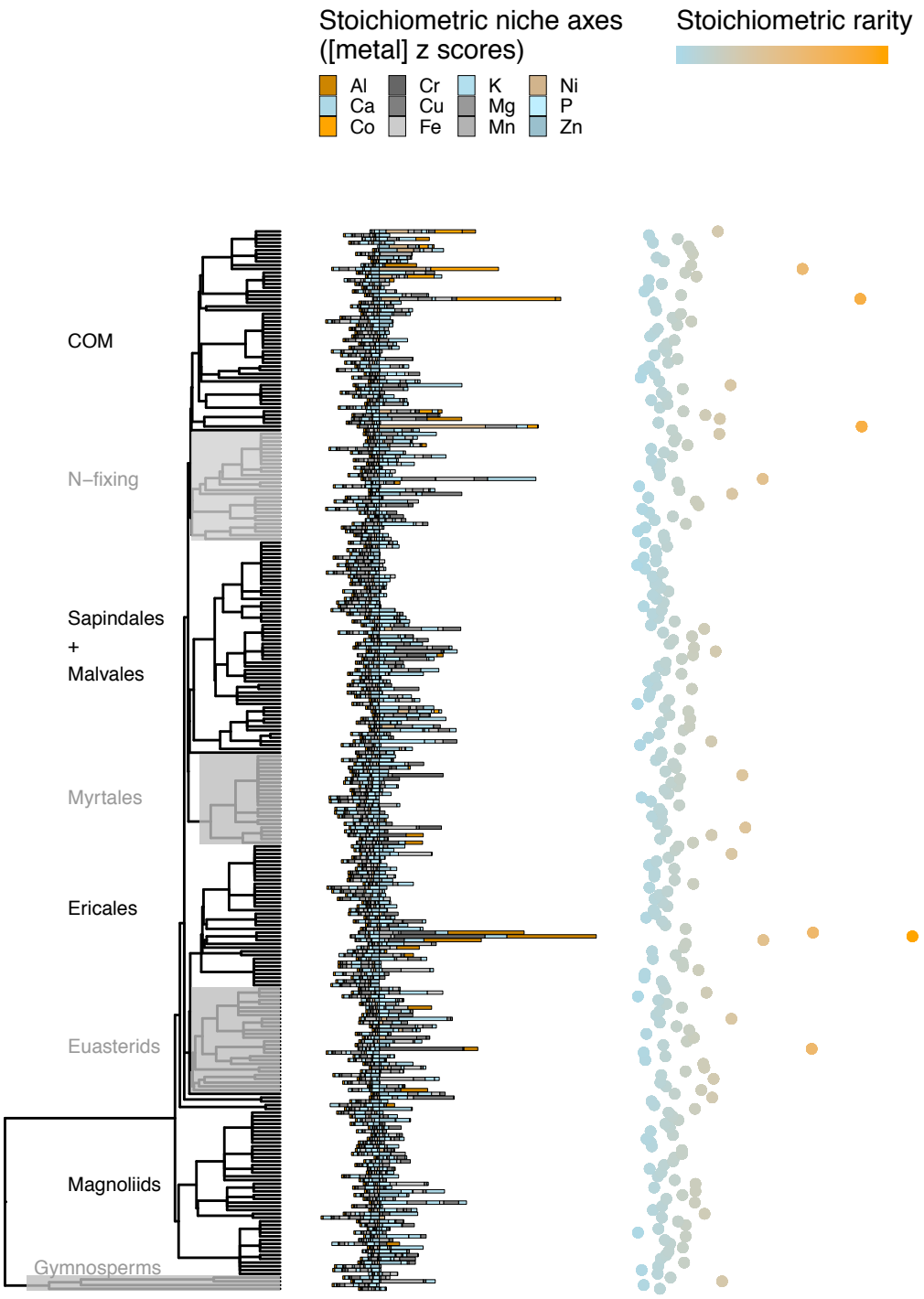


Fig. 6. Community phylogeny with horizontal stacked bars for all 12 metal elements scaled (z scores) and stoichiometric rarity points corresponding to each tip/species in the phylogeny.

3.4 Discussion

In line with our first hypothesis we, here, explicitly show the effects upon the multivariate stoichiometric niche of extreme edaphic heterogeneity as found across the island of Sulawesi. Whereas the functional structure of tropical forests has been shown to be influenced by macronutrient gradients (Asner et al. 2014), it is clear there is greater complexity to the underlying chemical drivers. This is intuitive on two counts, firstly, because plants are reliant upon a broad array of elements for fitness and secondly, because there are a number of elements found in soil deemed phytotoxic at sufficiently high concentrations (Andresen et al. 2018). This can then filter lineages that do not possess the physiology to persist on soils that exhibit such extreme chemistry which then leads to communities that covary in terms of stoichiometry and lineage occupancy across areas of heterogeneous soil. Lineage filtration may be caused by lineage failure to exhibit successful metal exclusion, toleration, accumulatory or hyper-accumulatory strategies. Likewise, those species that inhabit heavy metal rich soils may be outcompeted on the non-ultramafic soils by taxa better adapted to less extreme soils (Boyden et al. 2005). Thus, in contrast to our predictions 1a and 2, we have illustrated both phylogenetic and edaphic influences upon shifts in the stoichiometric niche occupied by the communities across the Sulawesi edaphic mosaic.

Plants occupying heavy metal rich soils exhibit physiological strategies including the exclusion or tolerance of small amounts of toxic heavy metals. The frequency of this strategy in tropical forest communities and how it manifests in multivariate stoichiometric space has previously been little studied. We here show

that many individuals exhibit this lack of extremity in foliar metal concentrations i.e. do not accumulate or hyper-accumulate metal and, as such, counter to prediction 1b, many species across soil types occupy similar regions of niche space (Fig. 1). Previous work on tropical trees has identified that most species occupy a core region of multivariate functional space (Umaña et al. 2017a) we here observe that this is reflected in the stoichiometric niche.

In contrast to our prediction 1c, PLS regression reveals that for the total stoichiometric diversity across our tree communities soil metal concentrations have a minimal impact upon species distribution along each separate stoichiometric niche axis, as most species are restricted to core stoichiometric values irrespective of edaphic heterogeneity. The stoichiometric stasis observed for most elements does not appear to be upheld when looking at Al, Ca and P where we find repeated strong positive relationships between these metals in soils and leaves. Specifically, strong positive effects of soil Al and P upon leaf Ca and soil Al, Ca and P upon leaf P. Positive correlations have been identified in tropical forests between these elements simply in terms of leaf chemistry (Masunaga et al. 1998, Metali et al. 2015) but also, as in our study, at the interface of leaf and soil (Asner et al. 2014). The complex relationship between the various physiological roles of these elements lead to a functional approach with higher growth rates for trees with greater Ca, N and P (Baribault et al. 2012). We also find evidence for heavy metal impact as soil Cr appears to have a strong negative relationship with leaf P. Negative effect of leaf P due to Cr exposure has been observed experimentally and is somewhat unsurprising as Cr ions compete with phosphate for shared cross-membrane transport proteins (Sinha et al. 2018). This

result indicates a role of soil Cr in the function of ultramafic plant communities, which has previously been given minimal attention, especially when compared with Ni. Although, generally, we find minimal effects of most soil metals upon leaf stoichiometric niche axes, where there are effects, the relationships are not simple i.e. soil metal X does not simply drive leaf metal X. The inter-relationships of metals for plant function (Kaspari and Powers 2016) appear therefore to manifest as an equally multi-faceted relationship between trees and soil.

In agreement with hypothesis 2 we have found that differentiation between communities across soil types is intimately linked to stoichiometric rarity. Rarity has been a theme well explored in terms of the frequency of individuals with the underpinning biology of these taxa well elucidated (Kunin and Gaston 1993), e.g. long-distance dispersal mechanisms are often favoured enabling fertilisation of distant conspecifics (Vermeij and Grosberg 2018). Comparative understanding of functional rarity is lacking (Grenié et al. 2017, Violle et al. 2017) - stoichiometric rarity even more so. There is no a priori reason for a rare species, in terms of number of individuals, to have a narrow abiotic niche (Gaston 1996). We show that this is not the case for stoichiometry, as concurrent with our prediction 2, we observe clear edaphic impact upon stoichiometric rarity whereby the presence of heavy metals in soils (i.e. a narrow edaphic niche on ultramafics) enables individuals to occupy a locus of stoichiometric space more distant from other individuals within the community (Fig. 5b).

The phylogenetic distribution of rarity has not been comprehensively examined, particularly for tropical plants (Loza et al. 2017). Exploring this in a stoichiometric context, we do not find support for our hypothesis 3b, as we

identify no evidence for phylogenetic constraint upon rarity. Whereas previously, stoichiometric rarity (in the form of metal hyperaccumulators) has been found in the tropics, to occur predominantly within the COM clade (van der Ent et al. 2018), within our study we have not identified such conservatism. This may be a result of Sulawesi's recent emergence compared to the other tropical study locations of New Caledonia and Borneo, i.e. we only observe two instances of hyperaccumulation (*Gironniera subaequalis* 10494 $\mu g\ g^{-1}$ Mn and *Sarcotheca celebica* 1077 $\mu g\ g^{-1}$ Ni) potentially due to temporal limitations on the evolution of this phenotype in Sulawesi and, as such, rarity within our study will tend to be those taxa that accumulate metals but not beyond the threshold formally denoting hyper-accumulation (e.g. 1000 $\mu g\ g^{-1}$ for Ni). Lack of hyperaccumulation could equally be due to low bioavailability of heavy metals in Sulawesi (van der Ent et al. 2016). Either way, the physiological constraints of accumulation compared to hyper-accumulation are such that the cellular mechanisms required for strategies tied to lower anatomical metal concentrations appear to occur across a greater breadth of the phylogeny than those that support hyper-accumulation.

We find that stoichiometric space occupation is driven by soil metals that are not those classically thought to drive plant function but by those more directly linked to plant toxicity. These metals at high concentrations can be detrimental via inhibition of photosystem function, auxin transport and uptake of other functionally crucial elements (Andresen et al. 2018). Despite these limitations, high concentrations of soil metals enable plants to exhibit accumulatory strategies most often via metal redistribution to relatively physiologically inactive regions of

foliar tissue such as vacuoles or the apoplast (Verbruggen et al. 2009). This physiology functionally differentiates the communities on heavy metal rich soils from those that do not. These species occupy niche space distant from most other species that to persist occupy a core stoichiometric niche. These distant or rare species are what ultimately differentiates the niche space occupied by communities on heavy metal rich soils from those that do not.

Analysis of the pairwise distances between individuals within and between communities revealed a significant effect of the 3rd soil metal PC axis, this axis is primarily responsible for a continuum from high Cr and Cu and low Co, Mn and Ni to high Co, Mn and Ni and low Cr and Cu. This results in distinction in niche space occupied across soil types but also between different ultramafic areas. This indicates that any perceived ultramafic filter is not homogenous i.e. one ultramafic area imposes constraints due to the presence of one subset of heavy metals whereas limitations of another area can be via another subset. If the different subsets exhibit toxicity via distinct intracellular pathways and the presence of mechanisms to combat heterogeneity in toxicity differ between lineages, the communities we find across the ultramafic soils have assembled within the context of very distinct environmental filters.

3.5 Appendix

Table A1. Soil principal component (PC) loadings for PC axes used in the analysis of foliar stoichiometry across forest communities in Sulawesi. Percentage of total edaphic variation explained by each PC axis is in brackets.

Metal	PC1 (45%)	PC2 (23%)	PC3 (12%)	PC4 (8%)	PC5 (7%)
P	0.12	0.45	0.09	0.02	0.02
K	0.19	-0.04	0.04	-0.08	0.94
Ca	0.14	0.44	0.03	0.00	-0.17
Mg	-0.19	0.03	0.27	0.84	0.13
Fe	-0.41	0.00	-0.24	0.05	0.03
Al	0.07	0.42	-0.04	-0.05	0.04
Mn	-0.35	0.07	0.43	0.02	0.06
Cu	-0.35	0.05	-0.32	0.04	0.07
Zn	-0.40	0.10	-0.14	-0.15	0.20
Ni	-0.34	0.01	0.40	-0.08	-0.07
Cr	-0.33	-0.05	-0.47	0.03	0.01
Co	-0.30	0.07	0.37	-0.49	0.03

Table A2. ANOVA results for the effect of soil (as PC axes) and phylogenetic dissimilarity (as forward selected eigenvector) upon mean and standard deviation pairwise distance in stoichiometric space within permanent plots established across Sulawesi. P values < 0.05 in bold.

	Mean			**Standard Deviation**		
Variable	**Df**	**F**	**P**	**Df**	**F**	**P**
Soil PC 1	1	12.3	**0.039**	1	77.71	**0.003**
Soil PC 2	1	1.13	0.366	1	3.79	0.15
Soil PC 3	1	10.5	**0.048**	1	25.58	**0.02**
Soil PC 4	1	0.86	0.421	1	0.81	0.43
Soil PC 5	1	0.05	0.838	1	1.83	0.27
Phylogenetic eigenvector 2	-	-	-	1	4.51	0.12
Phylogenetic eigenvector 5	1	0.30	0.624	-	-	-

Table A3. PERMANOVA results for the effect of soil (as PC axes) and phylogenetic dissimilarity (as forward selected eigenvectors) upon mean and standard deviation pairwise distance in stoichiometric space between permanent plots established across Sulawesi. P values < 0.05 in bold.

	Mean			**Standard Deviation**		
Variable	**Df**	**F**	**P**	**Df**	**F**	**P**
Soil PC 1	1	2.04	**0.02**	1	3.88	**0.004**
Soil PC 2	1	1.9	0.08	1	1.62	0.230
Soil PC 3	1	3.42	**0.001**	1	5.5	**0.002**
Soil PC 4	1	1.76	0.113	1	3.8	**0.030**
Soil PC 5	1	1.32	0.262	1	1.02	0.37
Phylogenetic eigenvector 1	1	2.11	**0.004**	1	1.19	0.32
Phylogenetic eigenvector 5	1	2.76	**0.005**	1	4.54	**0.01**
Phylogenetic eigenvector 7	1	1.28	0.226	1	1.04	0.47

4. Dispersal disequilibrium and stoichiometric niche breadth

Summary

When habitable areas become available to species post environmental change, there is a time lag until the novel areas are occupied. This is termed dispersal disequilibrium. The island of Sulawesi has formed recently, < 2 million years ago, via the agglomeration of a number of proto-islands. The link between the species niche and dispersal disequilibrium across regions once separated by seas is ill-defined. We specifically examine how the stoichiometric niche relates to dispersal across tropical tree communities in Sulawesi. We find that species occupying different soil types and regions in Sulawesi tend to occur in a broader stoichiometric niche than those species restricted to a single region and/or soil type. Conversely, clades that are overrepresented across different soil types and regions do not show greater niche breadth than those overrepresented on a single soil type and or region, indicating that both occupying a conserved and broad niche can promote dispersal. Using phylogenetic linear mixed effect models, we identify significant effects of both leaf Cr and Cu concentrations upon the abundance of species across Sulawesi, indicative of non-macronutrient niche axes as drivers of the composition of tropical tree communities.

4.1. Introduction

Following environmental alteration, e.g. glaciation, volcanic eruption or climate change; immediate dispersal by species to novel suitable areas does not occur, there is a time lag. This is termed dispersal disequilibrium (Svenning et al. 2015). The rate at which dispersal occurs is not consistent amongst clades (Eiserhardt et al. 2015). For instance, *Breynia* (Phyllanthaceae) clades differ in their capability to disperse eastwards across the Southeast Asian archipelago (van Welzen et al. 2015). The prevalence of dispersal disequilibrium on recently uplifted islands is not clear. For islands we would expect there to be a lag in dispersal from the earliest emergent areas to the later emergent areas. Additionally, an island may form via convergence of a series of separate islands. The ontogeny of Sulawesi provides a system to test for these legacy effects. The island formed from a number of proto-islands (earliest emergent areas > 20 mya) that only agglomerated to form the current landmass as we see it < 2 mya (Nugraha and Hall 2018). As such, we might expect regions that have uplifted at different times and later converged to not exhibit a homogenous flora despite suitable environment across the separate regions. Tests for dynamics such as these in tropical tree clades has as yet not been undertaken.

Filtering of lineages by the edaphic environment has regularly been observed across tropical plant communities (Tuomisto et al. 2003, Fine and Kembel 2011, Eiserhardt et al. 2013, Lehtonen et al. 2015). Edaphic heterogeneity drives turnover (phylogenetic beta diversity) by limiting the success of lineages maladapted to certain conditions (Fine et al. 2006). All of these studies take place within the continental Neotropics, the landmass of which, compared to Sulawesi,

has been largely constant for > 60 my (Seton et al. 2012). Additionally, the infertility of soils of the above Neotropical studies relates to the lack of macronutrients. Other soils impose different limitations upon plants via potentially toxic metal concentrations (Viehweger 2014). Ultramafic soils feature both a lack of macronutrients with abundant heavy metals including Ni, Co and Cr the largest tropical region of which is found in Sulawesi (van der Ent et al. 2013). The ultramafic outcrops of Sulawesi are intermixed with a mosaic of other soils leading to forests over, amongst others, limestone, sand, mafic and ultramafic substrates (Cannon 2005). How dispersal of tropical tree clades relates to both island ontogeny and extreme edaphic heterogeneity such as in Sulawesi is not known.

Studies looking at abiotic drivers of lineage turnover often identify overrepresentation of particular clades (Parra et al. 2010, Fine and Kembel 2011, Giehl and Jarenkow 2012, Lehtonen et al. 2015, Zappi et al. 2017). They identify nodes in a community phylogeny that have a greater number of descendant lineages compared to random draws from the breadth of the phylogeny (Webb et al. 2008). The weakness of this approach being that when one node has been identified to be overrepresented compared to the community wide null model all descendent nodes are likely to be identified as overrepresented and, as such, can obscure the nodes of interest for lineage turnover across communities (Borregaard et al. 2014). To overcome this, Borregaard et al. (2014) compare richness between sister clades against a null model specific to that node (specific overrepresentation score, SOS). This can then be used to deduce when one sister lineage is overrepresented on one side of a geographic or environmental boundary

and the other sister lineage the other (geographic node divergence, GND) (Borregaard et al. 2014). This provides phylogenetic insight into dispersal disequilibrium by identifying clades that are more diverse in one region or soil type but not another i.e. the lineage has not dispersed frequently to novel areas.

Heterogeneity in function between clades underscores dispersal disequilibrium via trait driven outcomes of interactions with biota and the environment. This permits that more distant occupiable environments are likely to be filled by species and clades that exhibit traits advantageous to dispersal and successful colonisation. This includes, plants with seed adaptations for distant dispersal, rhizomes (Miller et al. 2017), reproductive self-compatibility (Grossenbacher et al. 2017) and traits linked to fast growth rates (Negoita et al. 2016).

Functional traits are fundamentally linked to organism stoichiometry (Meunier et al. 2017). For example, leaf photosynthetic capacity is reliant upon N and P allocation (Wright et al. 2004) and plant defence is reliant upon defensive compounds (Endara et al. 2017). Stoichiometry can therefore be linked to dispersal by underscoring trait suites that permit dispersal success. Individuals that rapidly colonise suitable areas should thus exhibit stoichiometry advantageous for dispersal. Plant trait diversity is multidimensional in nature (Laughlin 2014) and is reliant upon equally complex stoichiometry (Kaspari and Powers 2016). This can be encapsulated by a point within multivariate chemical space, known as the stoichiometric niche (González et al. 2017). This derives from the classic niche concept of Hutchinson (1957) who depicted the niche as an n-dimensional volume. The niche dimension example illustrated by Hutchinson

depicts one axis that accounts for food size, which, for plants, parallels nutrient requirement and where Hutchinson lays out the reliance of taxa upon food size distributed within a lake, for plants, we can think of reliance upon nutrient heterogeneity across soils.

Plants that successfully disperse across we would expect to occupy a niche space that is advantageous for dispersal and subsequently establishment. The stoichiometric underpinnings of successful dispersal and colonisation of novel landmass and soil type is yet to be tested. Within an infertile and metal rich system as in Sulawesi, we might expect dispersal likelihood to correlate positively with stoichiometric niche breadth as the ability to tolerate variable physiological chemical concentrations will be advantageous when occupying environments of variable chemistry. This observation would not corroborate the often-observed phenomenon of phylogenetic niche conservatism (Losos 2008) whereby clades show minimal divergence in traits across constituent lineages. Stoichiometric niche conservatism may be observed, however, if physiological mechanisms prevent the differing soil chemistry of an unoccupied environment from impacting plant internal chemistry, with subsequently positive effects upon fitness.

We use data collected from a forest plot series across Sulawesi that covers three regions of differing ontogeny and four soil types to test the four hypotheses below:

Hypothesis 1) Dispersal limitation is primarily driven by legacy effects of island ontogeny.

Prediction 1a) Despite environmental similarity between regions, there is significant lineage turnover between them resulting in a high spatial component of phylogenetic beta diversity.

Prediction 1b) Sister lineages with discrepant overrepresentation are found between regions.

Hypothesis 2) Dispersal limitation is primarily driven by soil.

Prediction 2a) Despite distinct ontogeny between our three study regions, lineage turnover is greatest between soil types resulting in a high edaphic component of phylogenetic beta diversity.

Prediction 2b) Sister lineages with discrepant overrepresentation are found between soil types.

Hypothesis 3) Dispersal limitation is driven by the stoichiometric niche.

Prediction 3a) Species that occupy, and clades that are overrepresented on, more than one soil type and in more than one region exhibit wider stoichiometric niche breadth as greater flexibility in function permits occupation of environmentally novel habitat.

Prediction 3b) Leaf metal concentrations (i.e. each stoichiometric niche axis) drive the distribution of species across Sulawesi.

4.2. Methods

4.2.1. Sample collection and leaf and soil metal data

Samples were collected from the forest plot series and leaf and soil metal data quantified as outlined in Chapter Two.

4.2.2. Phylogenetic beta diversity and clade overrepresentation

Phylogenetic data derives from a plant family resolved supertree provided by Gastauer et al. (2017) and pruned to consist of the taxa identified across the entire plot series using Phylomatic (Webb and Donoghue 2005). The resolved phylogeny was then dated according to Magallón et al. (2015). Jaccard-like dissimilarity (beta diversity measure) between plot pairs across the series was calculated (Baselga 2017). To test predictions 1a and 2a, we modelled Jaccard-like dissimilarity against spatial and edaphic distance (the Euclidean distance between plots in a multivariate space consisting of the five soil PC axes) with permutation testing (999 permutations) to identify significance. We also performed variance partitioning to identify contributions of space and edaphic distance to the overall model.

As an added test of predictions 1a and 2a, we performed non metric multidimensional scaling (NMDS) of our Jaccard-like dissimilarity matrix with permutation tests (999 permutations) to quantify the significance of the five soil PC axes and region.

To test predictions 1b and 2b, we first calculated geographic node divergence scores (GND) (Borregaard et al. 2014) and those nodes with a score of > 0.6 were, following Borregaard et al. (2014), deemed to show disparity in sister lineages between communities. To test whether these sister lineages showed greater divergence between soil types or regions, we ran analysis of variance (ANOVA) tests with specific overrepresentation scores (SOS) as the response variable. Positive SOS indicates overrepresentation of one sister clade and negative SOS overrepresentation of the other. Significant difference in SOS values

between regions or soil types are indicative of the clades which drive the spatial and edaphic components of beta diversity.

4.2.3. Stoichiometric niche breadth and dispersal limitation

We first partitioned species that crossed region or soil type from those only found in one region or soil type. We then measured mean pairwise distances between individuals of each species within multivariate stoichiometric space. We then selected overrepresented clades by selecting clades from nodes with SOS of $> \pm 1.7$. Nodes with high SOS have one descendent lineage that is overrepresented within that community - these were the clades selected. We then partitioned these clades into those that were overrepresented across more than one region or soil type and those overrepresented in a single region or soil type. We then measured mean pairwise distances between individuals of each clade within multivariate stoichiometric space. To test prediction 3a, we performed non-parametric tests for differences in mean pairwise distances for both species (Wilcoxon) and overrepresented clades (Kruskal-Wallis) that were either restricted to a region or soil type or occur across regions or soil types.

To test prediction 3b, we examined how each stoichiometric niche axis (i.e. each leaf metal axis) drives the distribution of species across Sulawesi. We used a phylogenetic linear mixed effect model (PLMM). We specified region and site as random effects and incorporated phylogenetic covariance matrices to account for phylogenetic structure in stoichiometric niche axis values (leaf metal concentrations) and in species responses to the soil PC axes (Ives 2018). To ascertain p-values, likelihood ratio tests were performed for predictor variables

that had approximate p-values, from the original output, of < 0.05 following the recommendations of Ives (2018).

Most analyses were performed in R version 3.4.1 (R Core Team 2018). The phylogeny was dated with the Bladj algorithm in PhylcomR. Jaccard-like dissimilarity was calculated in betapart. Linear models and permutation testing were performed with ecodist. Variance partitioning was performed with code written by Swenson (2014). Nodiv was used to calculate GND and SOS scores. Mean pairwise distances in multivariate stoichiometric space were calculated with code written by Swenson (2014). Finally, PLMM was conducted with phyr in R version 3.5.1. (R Core Team 2018).

4.3. Results

4.3.1. Phylogenetic beta diversity and clade overrepresentation

Both spatial, and to a lesser extent, edaphic distance explained Jaccard-like dissimilarity between forest communities (Adjusted $R^2 = 0.55$, spatial $p < 0.001$, edaphic $p < 0.05$). This is exemplified by spatial distance accounting for 74 % of the variation, edaphic distance accounting for 19 % of the variation and the spatial/edaphic interaction accounting for the remaining 7 % of the complete model variance.

The two NMDS axes and permutation of environmental variables identified significant effects of the first soil PC axes ($p < 0.05$, all other PC axes $p > 0.05$) and region ($p < 0.005$, Fig. 1a) upon phylogenetic beta diversity. The soil PC axis with a significant effect upon (phylogenetic) beta diversity was responsible for a gradient of heavy metals but not macronutrients (Fig. 1b).

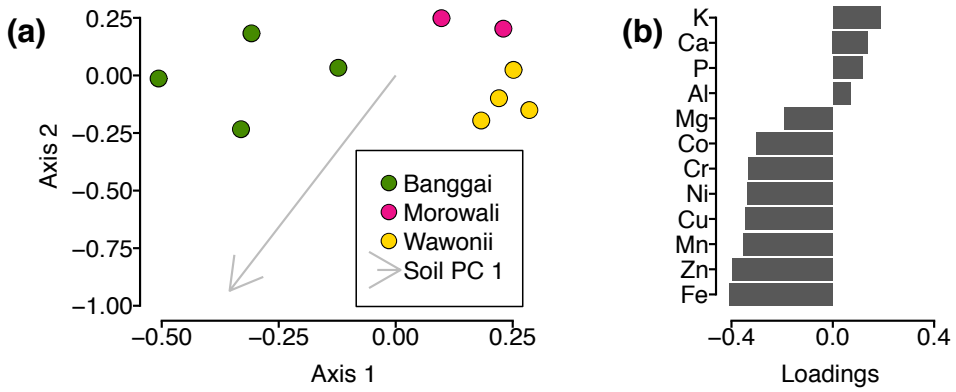


Fig. 1. a) Non metric multidimensional scaling (NMDS) axes of phylogenetic beta diversity. Colour represent thesignificant effect of region. Arrow indicates significant effect of the first edaphic principle component (PC) axis. b) Loadings of the soil PC axis that has a significant effect upon phylogenetic beta diversity.

We identify eight nodes with GND > 0.6 (Fig. 2). ANOVA tests of the SOS scores of these eight nodes show two nodes to have differences in overrepresentation of their descendent lineages between soil types and three nodes to have difference in overrepresentation of their descendent lineages between regions (all $p < 0.05$, Fig. 2).

Species that cross soil types show greater niche breadth than species on a single soil type ($W = 1506$, $p < 0.05$, Fig. 3). Species that cross regions show greater niche breadth than species found in one region ($W = 1750$, $p < 0.05$, Fig. 3). Clades overrepresented across soil types and or region did not exhibit greater niche breadth than overrepresented clades restricted to a single region and soil type ($\chi^2 = 0.819$, $df = 2$, $p > 0.05$, Fig. 4). Phylogenetic linear mixed effects models and likelihood ratio tests reveal a significant positive effect of Cr and Cu niche axes (leaf metal concentrations) upon species frequency across Sulawesi (Table A1). Additionally, Cr and Cu exhibited a significant interaction with both soil metal PC

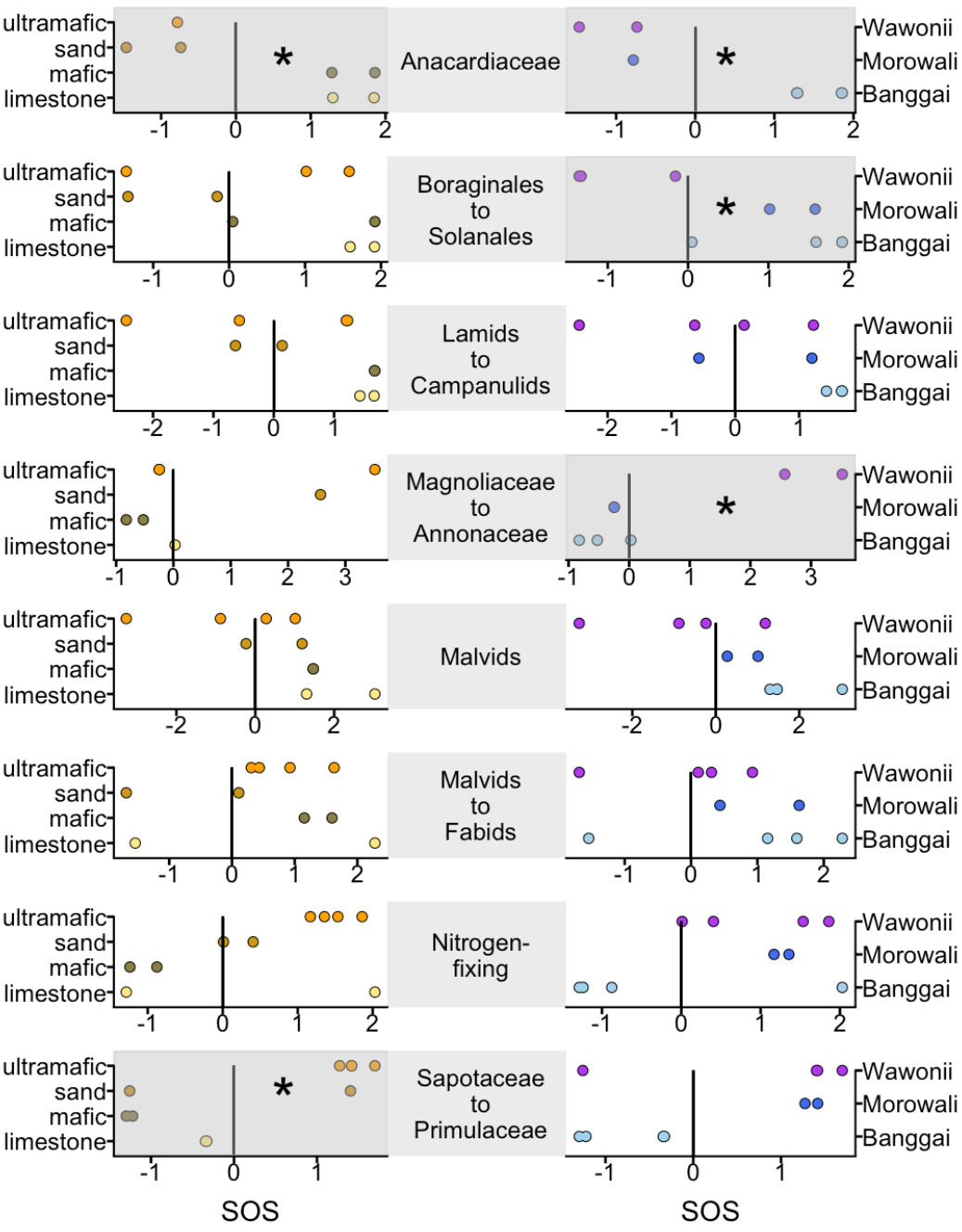


Fig. 2. Standard overrepresentation scores (SOS) of the eight nodes with geographic node divergence (GND) scores > 0.6. More negative scores indicate overrepresentation of one descendent lineage. More positive scores indicate overrepresentation of the sister lineage. * and grey shading indicate a significant effect of soil type (left hand side) or region (right hand side) upon SOS.

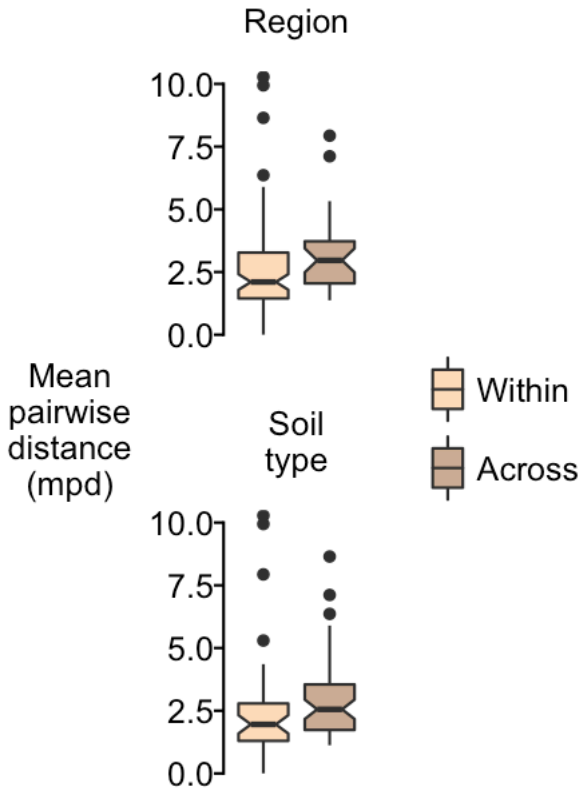


Fig. 3. Species stoichiometric niche breadth quantified as mean pairwise distance in stoichiometric space. Upper panel shows species found within and across regions. Lower panel shows species found within and across soil types.

axes 1 and 3 respectively, both axes account for variation in heavy metals (including Cr and Cu) rather than macronutrients (Tables A1, A2). Chromium also showed a significant interaction with soil metal PC axis 3, an axis of Al, Ca and P variability (Tables A1, A2).

4.4. Discussion

We find a significant spatial component of phylogenetic beta diversity. This is indicative of legacy effects of island ontogeny whereby the recent agglomeration of former proto-islands has created a highly heterogenous biota with minimal successful dispersal events between regions. The large spatial component of beta diversity may be suggested to be just that i.e. simply the prevalence of community distance decay (Soininen et al. 2007) however, in

Sulawesi, the magnitude of beta diversity appears greater than in other tropical forest systems at a similar scale (Condit et al. 2002, Dauby et al. 2014) which suggests more factors are involved i.e. legacy effects of island ontogeny. Our node divergence analysis shows that dispersal disequilibrium dynamics has different impacts between clades. There are three sister clades that show a significant difference in diversity between both clades between regions (Fig. 2). The pattern of overrepresentation between sister lineages is not spatially consistent, however. *Mangifera* is overrepresented in Morowali and Wawonii and its sister lineage *Semecarpus* overrepresented in Banggai (Anacardiaceae panel in Fig. 2) whereas the other two nodes that show discrepancy between regions represent a split between overrepresentation on Wawonii of one lineage and overrepresentation on Morowali and Banggai of the sister (Right hand side of 'Boraginales to Solanales' and 'Magnoliaceae to Annonaceae' panels, Fig. 2). The reasons for this lack of consistent pattern can be placed within the context of the nuances of

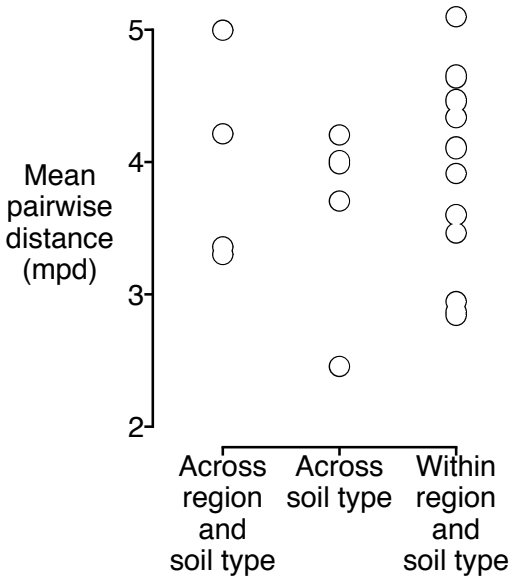


Fig. 4. Clade stoichiometric niche breadth quantified as mean pairwise distance (mpd) in stoichiometric space. Clade mpd shown for clades overrepresented; across regions and soil type, across soil type but within a region and within a region and soil type (no clades are overrepresented across regions but within a soil type).

Sulawesi's ontogeny. For instance, Morowali and Banggai are part of mainland Sulawesi at the axis and apex of the eastern peninsula respectively whereas Wawonii is an island off the southeast peninsula. The distinction observed for Anacardiaceae diversity between Banggai and the other two regions is likely due to the later emergence of this region c. 1 million years after both of the other two regions (Nugraha and Hall 2018). This clarifies the difference in legacy effects of ontogeny upon different lineages in Sulawesi.

We find a significant effect of the heterogeneity in the extreme soil chemistry across our plot series upon phylogenetic beta diversity. Node divergence analysis highlights an edaphic impact at two nodes with consistent distinction of overrepresentation between communities on ultramafic soils and those on mafic and limestone (left hand side of 'Anacardiaceae' and 'Sapotaceae to Primulaceae' panels, Fig. 2). In general, previous studies of tropical forest diversity have highlighted macronutrient impact upon community composition (e.g. Paoli et al. 2006), holistic approaches to encompass the numerous elements linked to plant fitness are infrequent (Kaspari and Powers 2016). Ordination results here show that soil variability in heavy metals, rather than macronutrients underlies the distribution of clades across Sulawesi (Fig. 1). This depicts that toxicity related elements (heavy metals) rather than classically defined growth rate limiting elements (macronutrients) can prove influential for the distribution of biota. Overall, we do not observe the predictions of hypotheses 1 or 2 but an interplay between both legacy effects of island ontogeny and the extreme edaphic mosaic of Sulawesi. This is indicative of the temporal aspects of range re-alignment following a significant event that shifts abiotic conditions, but also the role of

alternate environmental variables that may not be primarily associated with the event in question.

Relationships between niche dimensions and the distribution of plants have been seen for traits related to the major axes of plant function (LaManna et al. 2014). How multidimensional plant stoichiometry is linked to plant distributions beyond the study of plant macronutrients has lacked close inspection (Kerkhoff et al. 2006, Fyllas et al. 2009, Elser et al. 2010, Verboom et al. 2017 but see Asner et al. 2014 for more complex molecules i.e. phenols, lignin etc). When accounting for a dozen metal elements, we here show, in line with prediction 3a, that species distributed across soil types and regions generally show a broader stoichiometric niche compared to species restricted to a soil type or region (Fig. 3). Species niche breadth can thus be linked to legacy effects of island ontogeny whereby those species with reduced niche breadth are more likely to be dispersal limited and unlikely to occupy potentially suitable areas of Sulawesi that have uplifted at a different point in time. Variability in physiological metal concentration between populations has previously been observed (Pollard et al. 2014). We here find this to be advantageous for dispersal and establishment. A broader stoichiometric niche denotes either flexibility in internal metal concentrations due to cellular level tolerance strategies for a range of elements and concentrations and/or a species ability to facultatively exclude certain detrimental elements. This flexibility therefore promotes occupation of diverse environments.

Although we observe a statistical link between dispersal and species niche breadth, it is also clear that many species that do not cross regions and soil have

similar niche breadth to many species that do disperse (Fig. 3). This contradicts prediction 3a by identifying species that successfully occupy disparate areas and soil types exhibit narrow stoichiometric niche breadth/niche conservatism. Additionally, the similarity in niche breadth of many species with distinct range sizes is indicative of there being no a priori reason why a species restricted to a region or soil type may not show a broad stoichiometric niche particularly if flexibility in nutrient uptake persists within the meta-population (Assunção et al. 2003, Richau and Schat 2009) i.e. the two species with greatest niche breadth are restricted to one soil type on one region (outliers in Fig. 3).

Phylogenetic niche conservatism is a feature of a number of groups whether the niche be defined as the abiotic environment (Crisp et al. 2009) or as a trait suite (Wiens et al. 2010). We here bring together stoichiometric niche conservatism and dispersal disequilibrium to test whether clades that show limited legacy effects (clades overrepresented across regions and soils) differ from clades dispersal limited due to island ontogeny and edaphic heterogeneity (clades overrepresented within a single region and soil type). We find clades that are not dispersal limited to exhibit both stoichiometric niche conservatism and large niche breadth (following and opposing prediction 3a, Fig. 4). We therefore also find that these non-dispersal limited clades do not differ from dispersal limited clades which also show a continuum from stoichiometric niche conservatism to wide niche breadth (Fig. 4). This suggests that when we take the whole clade into account i.e. including species that are dispersal limited or not, there are multiple stoichiometric approaches that support dispersal in the face of extreme edaphic heterogeneity and restrictive island ontogeny.

When we account for species position along each niche axis independently (concentrations of each leaf metal) we find a positive impact of both Cr and Cu concentrations upon species abundance across Sulawesi. Leaf N and P have been intimated as key niche axes for the spread of taxa across spatial scales and the environmental heterogeneity this encompasses (Elser et al. 2010). Our results here show that by taking as holistic an approach as possible to plant stoichiometry, elements not thought of as those most limiting to plant function can prove influential for biogeography. It appears in Sulawesi that leaf macronutrient heterogeneity is not key to the distribution of species likely due to homeostatic constraint upon these metals due to their close ties to plant function i.e. significant variability on these niche axes are not permitted due to considerable decrease in fitness (Ågren 2008). Instead we find that alternate metals (Cr, Cu) can promote dispersal, establishment success and subsequently abundance across both regions with clear dispersal limiting factors between them (once separated by seas) in addition to heterogenous soils. This is presumably due to greater variance compared to macronutrient axes and thus greater possible proportional increase along niche axes for these elements which, in turn, provides a fitness differential along these niche axes.

Copper is crucial for a number of plant physiological processes including both photosynthesis and respiration and other processes key to tree function such as lignification (Burkhead et al. 2009). Conversely, copper can be highly toxic causing production of hydroxyl radicals that damage lipids, proteins and DNA (Cohu and Pilon 2010) so the ability to tolerate potentially damaging concentrations should provide related fitness benefits (Lange et al. 2017) whether

this is via herbivory prevention or by indirect fitness gains via not having to exclude the metal is not clear. The well documented mutagenetic effects of chromium ions (Sinha et al. 2018) suggests that Cr accumulation may be a more likely source of herbivory prevention than Cu or other accumulated metals such as Mg and Al.

We find that the effect of leaf Cr and Cu upon species abundance significantly interacts with soil PC axes 1 and 3 that are responsible for variability in heavy metal concentrations, indicative of increasing leaf Cr and Cu being advantageous for success on soils rich in heavy metals i.e. ultramafic. Additionally, we find that leaf Cr interacts with soil PC2 (Table A2) that is responsible for variability in Ca, P and K. This indicates that the identified advantageous Cr tolerance and accumulation strategies are coupled somewhat with not only Cr soil concentrations but also macronutrient availability. The specific interactions between leaf Cu and Cr and edaphic heavy metal PC axis are positive, however both soil Cu and Cr concentration negatively correlate with these PC axes, which suggests that either when these elements are low in the soil we find an exacerbated positive effect of leaf Cr on species abundance or that when these metals are low in leaves there is an increased positive effect of decreasing soil heavy metal. The positive interaction between soil PC2 and Cr is indicative of increasing impact of leaf Cr upon areas macronutrient low or, alternatively, a positive impact of increasing leaf Cr in low macronutrient environments. This shows that previously little comprehended soil and leaf metals can prove influential for tropical tree community composition. There is therefore a clear need for phytogeographical study linked to ecological stoichiometry to embrace the diversity of physiologically key elements at the plant-soil interface.

4.5. Appendix

Table A1. Phylogenetic linear mixed effect model output. Effect scores of each predictor variable with significant effects upon species abundance across the forest plot series in Sulawesi. Log likelihood values of the full model and subsequent models with predictor variables removed. Predictor values removed were those that had $p < 0.05$ from standard p-value tests. Likelihood ratio test (LRT) derived p-values from the full model and subsequent reduced models. Interaction terms are indicated with an ':' i.e. Cr:soil PC 1 is the interaction between leaf Cr and soil PC 1.

	Effect score	Log likelihood	LRT p value
Full model	NA	-1159	NA
Cr	3.8	-1173	< 0.001
Cu	0.4	-1167	< 0.001
Cr:soil PC 1	1.5	-1196	< 0.001
Cr:soil PC 2	2.9	-1163	< 0.05
Cu:soil PC 3	0.4	-1164	< 0.005

Table A2. Loadings of metal elements on the three soil principal component (PC) axes that significantly interact with stoichiometric niche axes (leaf metal concentrations) to drive tree abundance across the forest plot series in Sulawesi. Phylogenetic linear mixed effects models find that Soil metal PC1 and 3 positively interact with leaf Cr and PC2 with leaf Cu to drive species abundance across the plot series.

	PC1	**PC2**	**PC3**
C	-0.043	0.446	-0.166
N	-0.044	0.456	-0.052
P	0.118	0.446	0.086
K	0.189	-0.039	0.038
Ca	0.139	0.436	0.032
Mg	-0.192	0.030	0.271
Fe	-0.409	-0.003	-0.235
Al	0.070	0.419	-0.041
Mn	-0.352	0.073	0.431
Cu	-0.346	0.054	-0.324
Zn	-0.398	0.098	-0.139
Ni	-0.337	0.012	0.400
Cr	-0.335	-0.052	-0.472
Co	-0.302	0.072	0.369

5. The relationship between stoichiometric distinctiveness and species abundance is multifaceted

Summary

The determinants of species abundance within the context of ecological stoichiometry is little explored. Recent global analysis using functional traits as niche axes shows that common tree species tend to occupy a relatively similar or "core" position within multivariate niche space, whereas rare species often occupy regions of the niche hypervolume that are distinct from most other species. Using a forest plot series on the island of Sulawesi that covers sand, limestone, mafic and heavy metal rich ultramafic soils we assess species abundance and position in multivariate stoichiometric niche space. Here, each axis represents a continuum of metal element concentrations including both macronutrients and metals often accumulated by plants on ultramafic soils. We show that the relationship between species abundance and stoichiometric distinctiveness varies across space and scales. Whereby at a local scale a negative relationship between stoichiometric distinctiveness and abundance is observed in some but not all regions. At a greater scale, i.e. across the whole plot series, we find inconsistent relationships between total metal distinctiveness and abundance which exhibits no relationship and macronutrient distinctiveness and abundance which exhibits a negative correlation. This is indicative of macronutrient limitation upon species abundance whereas total metal distinctiveness, a phenotype which due to possible competitive advantages of metal accumulation is able to accumulate in communities.

5.1. Introduction

The species abundance distribution whereby communities constitute many rare, but few common species is a phenomenon consistently observed and, as such, interactions at the interface of abiota and biota that underpin this pattern are a key focus of ecology (McGill et al. 2007).

Enquiry into the causes of species rarity is complex and dependent upon the study system, scale and taxonomic group (Gaston 1994). Species may be numerically rare in the landscape because they arrive later and are unable to expand population size due to limitation by earlier established competitors with similar niche requirements (Chase 2007). Species may also however be rare via their existence in spatially restricted environments i.e. they have niche requirements that are not commonly available in the landscape (Kunin and Gaston 2012). These two predictions therefore have separate consequences for the niche proximity of species along the species abundance continuum (Umaña et al. 2017b). Specifically, under the former prediction we would expect both rare and abundant species to occupy proximate niche space. Whereas with the latter prediction we would expect to see rare species occupying niche space distant from most other species.

The latter prediction should also be scale dependent due to the likelihood that at increasing spatial scales more environmental heterogeneity will be encompassed, i.e. restricted environments locally will be more frequent at a greater spatial scale therefore niche requirements of species restricted locally should become more abundant with increasing spatial scale. This therefore should

manifest as a disappearance of the negative relationship between species occupying distinct niche space and species abundance with increasing scale.

The plant stoichiometric niche describes the ratio of elements that underpin plant function and consequently species interactions with both competitors and the environment that, in turn, leads to the frequency of that species within the environment (González et al. 2017, Meunier et al. 2017). Foremost, this is via the macronutrients that covary with many of the best studied plant traits such as height and specific leaf area (Wright et al. 2004, Díaz et al. 2016).The stoichiometric niche has the added advantage of accounting for metal accumulation plant strategies that may provide functional advantage from provision of suitable heavy metal rich habitat for conspecific recruitment via localised leaf litter decomposition, herbivory deterrence and pathogen defence (Boyd 2004) but, equally, must provide significant limitations due to the toxicity of these metals and the requirement for them to be translocated to relatively inactive areas of the plant (Deng et al. 2018). We here use the stoichiometric niche concept to define how complex tropical tree chemistry relates to the species abundance distribution.

The island of Sulawesi is formed of an edaphic mosaic that includes the largest expanse of ultramafic soils in the tropics (van der Ent et al. 2013). Ultramafic soils are heavy metal rich substrates that geologically derive from historically exposed mantle. These areas frequently exhibit species that accumulate metal. If stoichiometric distinctiveness on Sulawesi is driven by species that accumulate metals on ultramafic soils, we might expect these accumulators to be rare components of the community and, as such, total

stoichiometric distinctiveness, i.e. including metal accumulation, should follow similar patterns to macronutrient distinctiveness which links more directly to classic measures of plant function. We specifically test three hypotheses:

Hypothesis 1) Rare species occupy distinct stoichiometric niche space whereas common species occupy core niche space.

Prediction 1a) There is a significant negative relationship between stoichiometric distinctiveness and abundance at local scales.

Prediction 1b) At larger scales there is no relationship between stoichiometric distinctiveness and abundance due to large scales encompassing many landscapes that support broad stoichiometric niche requirements.

Hypothesis 2) Rare species are outcompeted by common species occupying a similar stoichiometric niche.

Predictions 2a) There is no relationship between abundance and stoichiometric distinctiveness at a local scale.

Prediction 2b) At larger scales we continue to find no relationship between abundance and stoichiometric distinctiveness.

Hypothesis 3) Metal accumulation and macronutrients have similar impacts upon the species abundance distribution.

Prediction 3) The relationships observed between species abundance vs total metal stoichiometric distinctiveness and species abundance vs macronutrient distinctiveness do not differ.

5.2. Methods

Leaf samples were collected, and species abundance calculated across the forest plot series previously outlined. This encompasses three separate regions and forests over limestone, sand, mafic and ultramafic substrates. Seven hundred and twenty-three leaf samples (c. 100 mg) were digested in 10 ml of concentrated nitric acid using a CEM Mars Xpress microwave and made up to 100 ml in ultrapure (18 MΩ) deionised water. Al, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Ni, P and Zn concentrations were quantified using a Thermo-Finnegan iCAP 6300 Duo inductively coupled plasma optical emission spectrometer.

One hundred and one species were sampled multiple times in each plot, the mean for each species within each plot was used for further analysis alongside all species sampled once per plot. Principal component analysis of all individual leaves with scaled data (z-scores) indicated that > 90 % of the variation was explained with the inclusion of nine principal component axes - we therefore retain the original scaled data as axes for further analysis.

We quantified stoichiometric distinctiveness as the mean distance in multivariate space between a species and all other species within the community, following the approach used by Grenié et al. (2017) for functional trait space. We used a multivariate space composed of all 12 leaf metal elements to quantify total metal distinctiveness. We used a multivariate space composed of Ca, P, K, Mg to quantify macronutrient distinctiveness.

Following Umaña et al. (2015) we then calculated Pearson's correlation coefficients to identify significant relationships between our two distinctiveness measures and log-transformed species abundance. A significant negative

relationship is indicative of abundant species existing in core stoichiometric space whereas less abundant species tend to exist in distinct stoichiometric space. To test the scale dependence of this relationship, we first performed the analysis for each of our three study regions, this represented the relationship at a local scale. For comparison at a larger scale, we then tested for a relationship across the complete plot series.

5.3. Results

At local scales we find a negative relationship between total metal (all 12 metals) distinctiveness and species abundance on Wawonii ($t=-2.31$, $r=-0.17$, $p < 0.05$) but no relationship in Morowali ($t=-1.22$, $r=-0.13$, $p > 0.1$) or Banggai ($t=-0.214$, $r=-0.016$, $p > 0.5$). At this scale we also find a negative relationship between macronutrient distinctiveness and species abundance on Wawonii ($t=-3.49$, $r=-0.245$, $p < 0.001$) but not in Morowali ($t=0.813$, $r=0.093$, $p > 0.1$) and Banggai ($t=-0.326$, $r =-0.02$, $p > 0.5$).

Across the full plot series, we find no significant relationship between total metal distinctiveness and abundance ($t=-1.43$, $r=-0.07$ $p > 0.1$, Fig. 1a). Macronutrient distinctiveness however, did show a significant negative relationship with species abundance ($t=-3.97$, $r=-0.184$, $p < 0.01$, Fig. 1b).

5.4. Discussion

At local scales the relationship between stoichiometric distinctiveness and abundance was not consistent across our three study regions. On the island of Wawonii those species that exist in core niche space tend to be common whereas

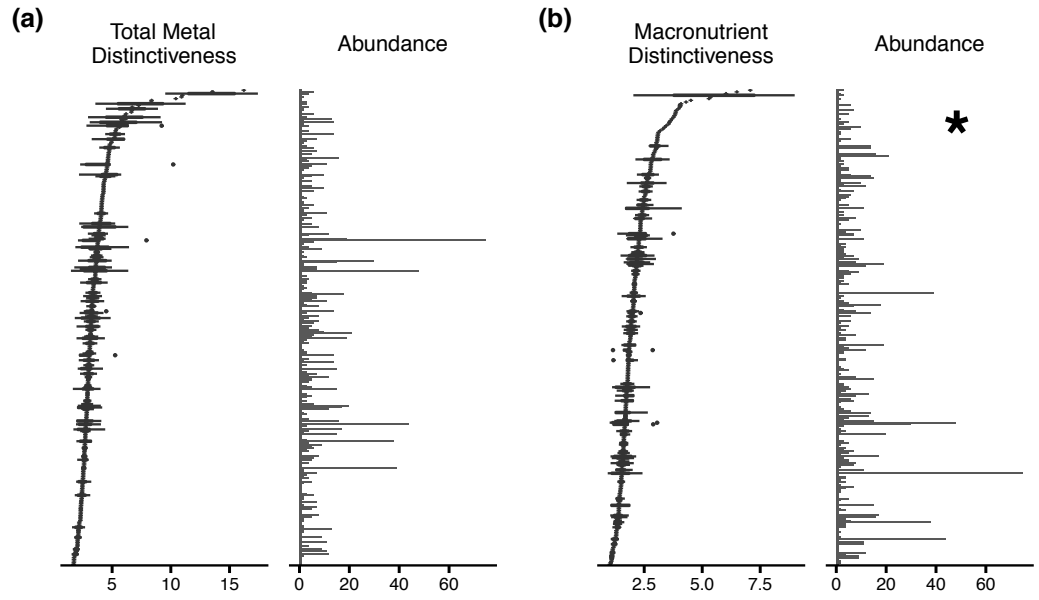


Fig. 1. The relationship between species abundances and a) total metal distinctiveness (12 metallic elements) and b) macronutrient distinctiveness (Ca, K, P, Mg) in forest communities across Sulawesi. Asterisk denotes significant negative relationship ($p < 0.01$) identified by Pearson correlations.

those species in distinct niche space tend to be rare, indicative of these species occupying niche space with requirements that are not readily available across the region (this supports prediction 1a).

For our other two regions we do not observe a relationship between distinctiveness and abundance indicative of our prediction 2a) that species occupy similar niche space whether common or rare and, as such, rarity may be a consequence of when the species established i.e. earlier establishment supports greater abundance or equally may be due to other traits that our leaf metal dataset may be a poor proxy of such as dispersal mode or symbiotic associations. At local scales, the pattern is consistent across both total metal and macronutrient distinctiveness suggesting that at this scale the limitations of being

stoichiometrically distinct is consistent whether exhibiting a functional approach underpinned by macronutrient or total metal concentrations. Presumably, this relates to the environment in these regions which provide suites of soil chemistry that supports similar plant stoichiometric approaches (i.e. core or distinct) irrespective of the leaf metals in question.

At a larger scale, across the entire plot series, we do not find a negative relationship between total metal distinctiveness and abundance consistent with our hypothesis 1b). Thus, as we increase the area of Sulawesi analysed we encompass more areas that support distinct niche space. Variability in metal concentrations in plants is an order of magnitude greater for heavy metals than macronutrients as the former can be both excluded and hyper-accumulated by plants whereas plant function requires macronutrient concentrations to be somewhat constrained to retain homeostatic integrity (Meunier et al. 2014). As such, for interspecific differentiation in stoichiometric ratios the continuum of heavy metal concentrations is of far greater consequence for distinctiveness with regard to the stoichiometric niche. It is therefore unsurprising that as we survey larger scales in Sulawesi and increase the area of heavy metal rich soils covered, the relative abundance of distinct species increases.

Whereas the negative relationship between total metal distinctiveness and species abundance is not present at large scales for macronutrients directly opposing predictions 1b, 2b and 3a we observe a significant negative relationship between distinctiveness in niche space and abundance. Thus, it appears that differentiation from the core macronutrient space occupied by plants poses limits upon the population sizes of these species. A similar relationship has been

observed across global tree communities and occupied trait space (Umaña et al. 2017b) across life history stages (Umaña et al. 2015, 2017a). If macronutrients underpin the variability in the functional traits that are key to community assembly then it appears that even across regions of edaphic heterogeneity stoichiometric ratios that support a core functional approach are key to becoming abundant in an environment. Greater macronutrient distinctiveness may also limit species abundance due to it being representative of a departure from stoichiometric homeostasis that underpins optimal plant function. The clear linkage between macronutrients and their role in enzymatic function key to cellular level processes would be the most obvious reason for this. Macronutrient distinctiveness could also, for some species, be an artefact of a stoichiometric trade-offs, where to accumulate/tolerate or exclude heavy metals, a distinct macronutrient ratio is required.

Macronutrients and the most often measured plant traits such as wood specific gravity, tree height and specific leaf area do not consider metal accumulatory strategies that have the potential to provide competitive advantages. This may, as we have observed in this study, lead to distinct accumulator species reaching relatively high abundance in the flora. This is indicative of a multi-layered relationship between plant stoichiometry and biogeography, without even beginning to uncover the relationships between abundance and more complex plant defence compounds such as the phenolics and alkaloids that are involved with tropical tree and herbivore interaction (Volf et al. 2018).

6. Ecological conclusions from a biogeographic juncture

> '*The anomalies and eccentricities in the natural history of Celebes ……. presents us with a most striking example of the interest that attaches to the study of the geographical distribution* (of species)' Wallace (1869).

In this thesis, we have shown that Sulawesi's ontogeny and edaphic heterogeneity have combined to shape the distribution of its tree species. We have found evidence for considerable dispersal disequilibrium following island agglomeration from proto-islands and that the high turnover induced by regions being previously separate is interlinked with edaphic heterogeneity. Across the extreme variability of these soils, we find a consistent accumulation of diversity, thus it is notable that the extreme limitations of ultramafic soils do not lead to limited tree diversity. This differs from ultramafic systems elsewhere (Proctor 2003).

For elements that influence plant function, the interface between plants and soil is complex; this has been clearly understood within agricultural systems but for far more diverse tropical plant communities impacts across the multitude of elements lacks quantification (Kaspari and Powers 2016). Studies of tropical forest stoichiometry have generally been restricted to those macronutrients deemed critical for plant function (Townsend et al. 2007). The heavy metal rich ultramafic soils of Sulawesi have enabled a more thorough understanding of the metallic chemistry of tropical floras. Our work, alongside other recently compiled

datasets (Reeves et al. 2018, van der Ent et al. 2018), allows us to better quantify the relationships between plant metal concentrations and plant diversity.

This thesis has embraced the advantages of the duality of the Hutchinsonian niche concept (Colwell and Rangel 2009). Hutchinson (1957) conceptually separated the species niche from species distribution in the environment. This has enabled us to test the effects of the environment upon the stoichiometric niche of species and the effects of species stoichiometric niche upon their distribution across Sulawesi.

We have found that species tend to occupy a similar core stoichiometric niche that likely underpins a core functional approach of most members of a community (Umaña et al. 2017a). A small proportion of species do, however, inhabit distinct niche space that is driven by soil heavy metal concentrations rather than macronutrients. These heavy metals found at high concentrations in ultramafic soils also drive differences in stoichiometry at the community level. In addition, it appears that these shifts are related to lineage turnover between communities whereby a change in community assemblage across soils covaries with a change in the occupied niche.

If we then take the approach of looking at the impact of a species' stoichiometric niche upon its distribution, we have seen that, in general, a broader niche is linked to broader spatial and edaphic distributions. However, we find that this pattern does not hold at deeper phylogenetic scales whereby clades that are diverse across both soil types and regions in Sulawesi do not have greater niche breadth than those clades that are diverse but restricted to a single region and/or soil type. This shows, clearly, that diverse stoichiometric strategies can prove

successful for occupation of an extreme edaphic mosaic as found in Sulawesi. This is corroborated by the failure to find a negative relationship between stoichiometric distinctiveness and species abundance across our forest plot series.

Our results provide the broadest plot-based quantification of the impact Sulawesi's abiota upon its tree communities. Biogeography in archipelagic Southeast Asia has been primarily approached from a biotic perspective whereby species distributions have driven conclusions regarding areas of floristic and faunal similarity (Simpson 1977, van Welzen et al. 2011, Holt et al. 2012). General consensus supports a tri-regional system with the amalgamative zone of Wallacea flanked by the biotically Asian Sunda and the biotically Australian Sahul regions. The three regions belong largely to a single biome - the wet tropics (although there are also some seasonal areas). Within other better studied non-archipelagic wet tropical systems, limits to dispersal appear minimal (Pennington and Lavin 2016, Dexter et al. 2017). The obvious factor that underlies the differentiation within the wet tropical biome in Southeast Asia is its archipelagic nature. Despite this, recent dispersal events for a number of plant lineages across the central Wallacean region suggest the archipelago is no barrier to occupation of the breadth of Southeast Asia (Crayn et al. 2015, Yap et al. 2018). Within the broader context of widespread Neotropical dispersal, many abiotic aspects prove limiting for dispersal and drive discrepancy in species distribution (Draper et al. 2017, Bemmels et al. 2018). For Southeast Asia, a similar ecological understanding is lacking but recent work by Yap et al. (2018) has begun to address this by linking plant function to climate and propensity for dispersal into tropical Australia from Southeast Asia. If the archipelagic nature of the Sunda-Wallacea-Sahul system is

the key difference affecting dispersal dynamics compared to continental settings, the impact of the abiota of these islands and particularly their soils, cannot be ignored. Sulawesi is the largest island in Wallacea, it is located at the axis of the clearest floristic demarcation in the region, Dipterocarp forests dominate the adjacent Sundaic island of Borneo but not Sulawesi. The biotic impact of the abiotic facets of Sulawesi are therefore crucial to understanding the region's macroecology. We have illustrated here a fundamental physiological impact, upon lineages, of the island's extreme edaphic mosaic. This, in conjunction with Sulawesi's areas of rain shadow and high proportion of landmass dominated by uplands compared to surrounding islands, may prove influential for historic dispersal; this, however, remains untested.

Many biogeographers have followed Wallace in emphasizing the consequences of the historic separation of Australia and Asia upon the biota of the Southeast Asian archipelago (van Welzen et al. 2011). Wallace did not make land on the two eastern peninsulas of Sulawesi. Our study of these regions has made it clear that the abiotic influence of the islands within Wallacea can impact plant physiology and subsequently their geography. As such, an expansion of the understanding of the abiotic environment across the archipelago will be key to unpicking the reasons for the distinction in plant communities from New Guinea to the Malay Peninsula.

Numerous environmental variables can be envisaged to impact upon the region's plant geography. Regions of soil that pose challenges for plants are considerable. Karstic limestone outcrops across all island chains (Clements et al. 2006). There are ultramafics, such as those studied on Sulawesi on Borneo, the

Moluccas and New Guinea (Galey et al. 2017). The extent of infertile sandy soils is not clear; for instance, we found extensive areas of sandy soils on Wawonii island that were demarcated as alluvial on habitat maps (Cannon et al. 2005). If sandy soils are more widespread across the archipelago than currently known (they have been previously identified in Borneo, e.g. Brünig 1974) they may prove influential for plant distribution, as they have in both Amazonia (Fine and Kembel 2011) and Sundaland (Slik et al. 2011). The relative proportion of each island that is upland (and conversely lowland with associated edaphic and climatic gradients) differs across the archipelago, suggesting that competition for areas that support different portions of elevation linked niche space will, equally, differ considerably across the archipelago. Sulawesi exhibits areas of rain shadow that have been documented, i.e. Palu is one of the driest cities in Indonesia (Whitten and Henderson 2012). This could prove influential for biogeography if we consider the lack of dispersal between Neotropical wet and seasonally dry forests, with clades exhibiting niche conservatism either side of the climatic barrier (Pennington and Lavin 2016). The vast extent of lowland Borneo is aseasonal; if lowland seasonal pockets are frequently nested within the rest of the wet tropical areas of the archipelago, they could prove a significant, but as yet, unconsidered microclimatic barrier to dispersal. Similarly, the drier chain of islands from Java to Timor have not been adequately examined from a dispersal perspective. This dry island chain is a good example of how these abiotic variables might interact with other environmental variables to influence regional phytogeography. For instance, the East Java and the Lesser Sundas are dry, i.e. climatically limiting, whereas Sulawesi and the Moluccas feature significant ultramafic outcrops, i.e. edaphically limiting.

It is not a huge leap of the imagination to envisage how these factors in conjunction (the islands mentioned span the breadth of the archipelago, Fig. 1) could restrict floristic admixture between Asia and Australasia

There are marked boundaries in zoogeography in the Southeast Asian archipelago whereby islands are startlingly either Asian or Australian despite their proximity such that when discussing Bali and Lombok Wallace (1869) exclaimed that:

> '*the strait is here fifteen miles wide, so that we may pass in two hours from one great division of the earth to another, differing as essentially in their animal life as Europe does from America*' and this despite the islands being '*subjected to the same climate, and bathed by the same oceans*'.

Many of the islands have been emergent for at least 5 million years (Hall 2013). For the zoographical distinction observed to have remained during these periods, the resilience to invasion of these communities must be significant. This resilience

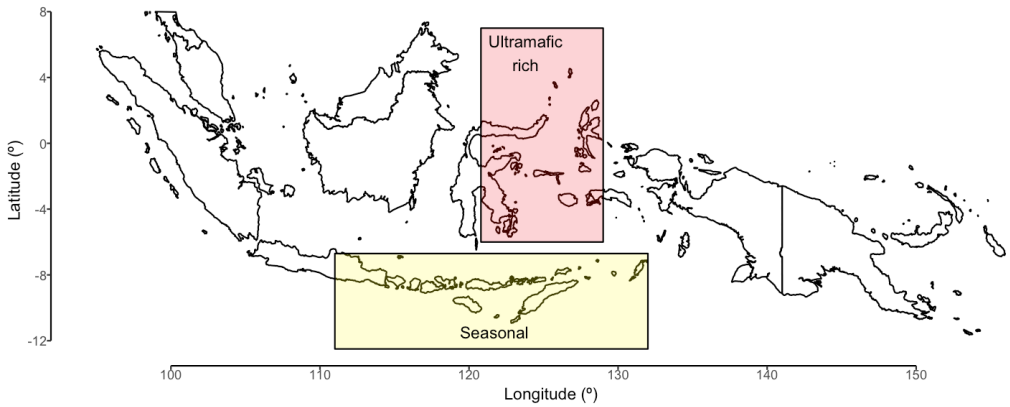
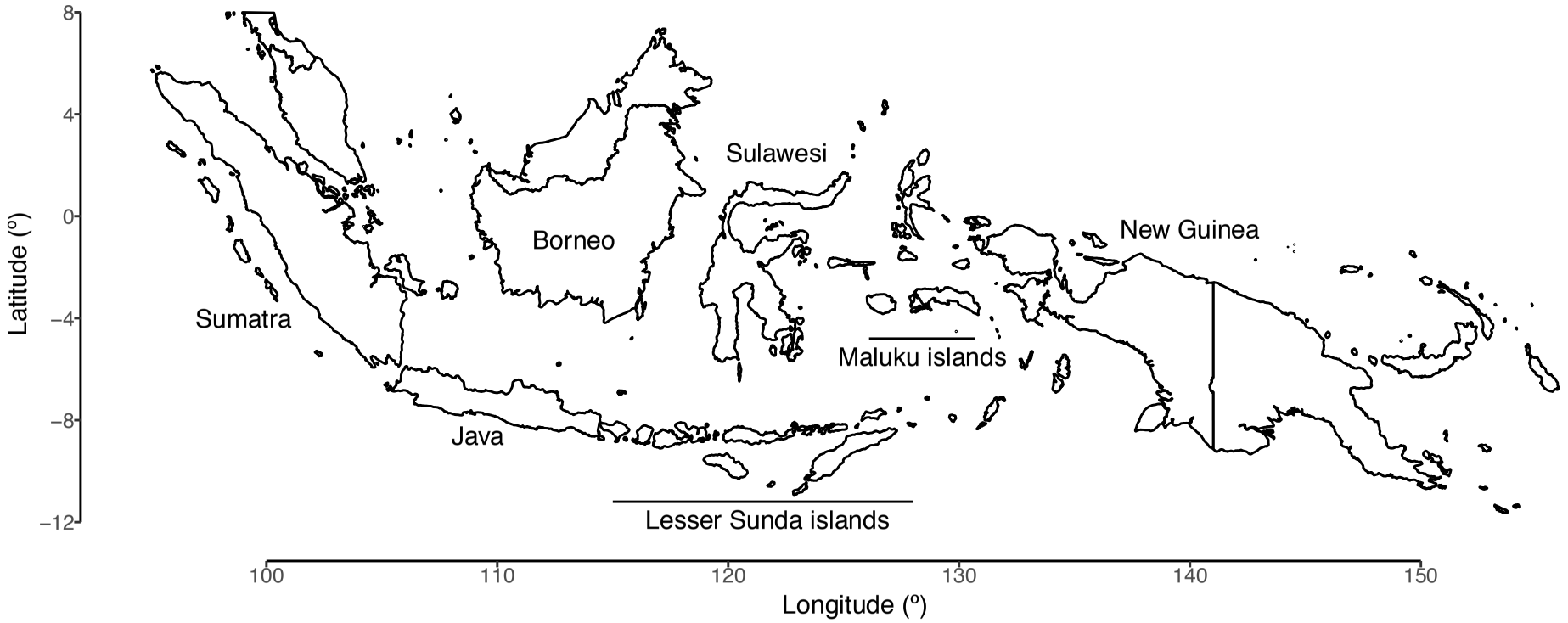


Fig. 1. Map of the Southeast Asian archipelago with islands with significant ultramafic outcrops in red and islands with a significant dry season in yellow.

will be tied to local fauna outcompeting arriving propagules due to the communities of inhabitant fauna being better adapted for persistence within that island's particular plant community. If these tropical plant assemblages are a consequence of abiotic filtering, as they to some degree inevitably are, then generally all biogeography in the Malay Archipelago may be underpinned by environmental variables rather than the historic separation of Australia and Asia.

7. Map of the Southeast Asian archipelago



8. An enigmatic genus on an enigmatic island: The re-discovery of *Kalappia* on Sulawesi

The Indonesian island of Sulawesi possesses a biota defined by both anomaly and intrigue. It has high levels of endemism (Michaux 2010) but, despite attracting research interest since the time of biogeographic pioneers such as Alfred Russell Wallace, the island remains relatively undocumented (van Welzen et al. 2011) with collection rates below much of the wider region (Kessler et al. 2002). There is discrepancy when assigning the island to a biogeographic unit, the current known flora tends toward a placement within the Austral-Asian amalgamative region of Wallacea, which encompasses the chain of islands between Borneo and New Guinea (van Welzen et al. 2011).

The region has been designated a biodiversity hotspot and Sulawesi, as the largest landmass within Wallacea, is therefore critical to successful conservation of its diverse fauna and flora (Cannon et al. 2007). Extraction of both gas and valuable metal ore deposits is a major contributor to deforestation in Sulawesi, particularly mining of nickel, across the 15 400 km^2 ultramafic outcrop (c. 8.8 % of total land area) (van der Ent et al. 2013). Extraction is most prominent in the Soroako area close to the town of Malili (Fig. 1). A number of botanists including Meijer, Reppie and van Balgooy visited Malili from the 1930s to the 1970s. Amongst the collections made were less than ten specimens of a legume tree species from a very small area of wet tropical forest. This was described as *Kalappia celebica,* as the single species in the genus (Kostermans 1952). The taxon exhibits anthers that dehisce via a pair of apical pores. This characteristic is rare in

legumes but observed in other closely related taxa and is indicative of buzz pollination by bees (Tucker 1998). The anthers of *Kalappia* also feature a prominent spur that extends from the base of one of the two apical pores (Fig. 2). This combination of characters is apparently unique to *Kalappia*.

Kalappia has been exploited for use in house construction, ship-building and in furniture manufacture. Even prior to scientific description of the species, timber export to Makassar, the largest city in Sulawesi, had been observed by Kostermans (1952). This evident threat to the species coupled with its restricted distribution led to an IUCN red list conservation assessment of 'Vulnerable' (IUCN 1998). A lack of collections since the 1970's gave rise to the suspicion that the taxon was likely endangered (Lewis 2005) and potentially extinct.

In 2010, two sterile herbarium specimens of a tree from the Kolaka area of Sulawesi (Fig. 1), with the local name "kelapi" were tentatively identified as *K. celebica* by Dr Elizabeth Widjaja and accessioned in Herbarium Bogoriense (BO).

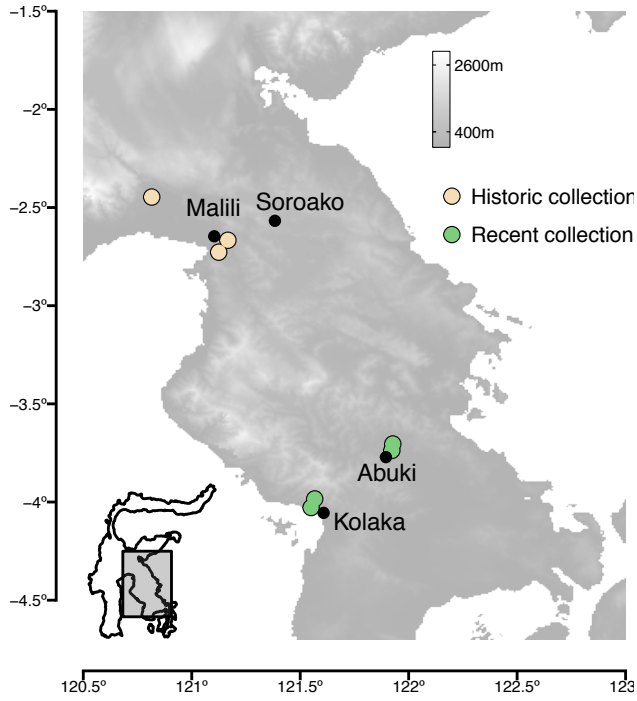


Fig. 1. Map of collection localities for *Kalappia celebica* in Sulawesi. The collections around Malili are highly threatened due to nickel mining. The Kolaka collections are the only two trees left in the vicinity. The Abuki collections are from a copse of trees retained for the honey bees they support and another population that is threatened due to logging.

The Kolaka region is approximately 140 km south of the original collection area of the species near Malili. In 2016, we visited a deforested area further inland near the village of Abuki (Fig. 1) where at least 20 trees are retained for the honey-producing bees that frequent them. Additionally, forest near Abuki was visited; where *K. celebica* was observed to be a notable component of the tree community with 20 mature trees observed within c. 2.5 ha. A number of individuals were in flower (Fig. 2) allowing floral dissection, comparison and verification that these trees were indeed a new spatially distinct population of *K. celebica*.

Following these new observations (collections: Trethowan 707–721 lodged in the herbaria at Kew (K) and BO), we update *K. celebica*'s previous IUCN assessment (IUCN 1998) with a new preliminary conservation assessment. We calculated extent of occurrence (EOO) and area of occupancy (AOO) using herbarium specimen point data mapped in GeoCat (Bachman et al. 2011) based upon 19 herbarium specimens (Trethowan 707–721, Widjaja 9618 and 9901, Meijer 11256, Neth. Ind. For. Service bb.32456, Boschproefst. bb.13572) from K, BO and the digitised collections of Leiden (available at: http://bioportal.naturalis.nl). An EOO of 6460 km^2 (IUCN category Vulnerable) is indicative of *K. celebica* inhabiting a wide area. Landsat data indicates that there are large tracts of relatively inaccessible wet tropical forest in good condition between the currently sampled localities (Cannon et al. 2007), inhabiting similar soil types and elevational range to known *K. celebica* populations. These areas have not been surveyed by the authors, nor to our knowledge during other collecting trips, but represent potential suitable habitat for the species, possibly harbouring additional populations. The AOO of 28 km^2 (IUCN category

Endangered) does not take this potential presence into account and is thought not to represent the total area occupied by the species. Therefore, the assessment here is based upon EOO results.

Threats are posed at each of the three collection localities (Abuki, Malili and Kolaka). The population near Abuki is highly threatened due to its presence in 'Hutan Produksi' or production forest where individuals are legally harvested for timber. Based upon our observations, no regeneration programme is facilitated locally. The copse of *K. celebica* retained for honey production in Abuki is privately owned, where threat arises from potential redirection in the business model induced by productivity decline or fluctuation in demand for honey. The population around Malili has not been visited by recent collecting trips and whether a viable population remains is unknown. The expanding human population and mining activities (e.g. ongoing nickel extraction by the Brazilian

Fig. 2. Foliage, inflorescence (a), flowers (b) and spurred porate anthers (c, d) of *Kalappia celebica* collected near Abuki village, Sulawesi. Photo (a) courtesy of Alvin, undergraduate at Universitas Halu Oleo, (b) was taken by LAT. Images (c, d) were recorded with a Hitachi S4700 field emission scanning electron microscope.

mining company Vale) in this region decrease the likelihood of this. Following personal observation (LAT) and conversation with local villagers, it became clear that the collections near Kolaka derive from the only two trees left in the vicinity, one of which is in a private garden where the owner is yet to allow the tree to be felled for timber, despite lucrative offers, and the other in a nearby tourist park. If we remove these two individuals near Kolaka from the conservation assessment on the assumption that they do not represent a viable population, this results in a much smaller EOO (1495 km^2) and AOO (20 km^2), which correspond to an Endangered categorisation. However, here we follow the categorisation based upon EOO of all individuals, the area of which covers a greater proportion of the expanse of forest where *K. celebica* is likely to inhabit, and we therefore designate *K. celebica* as Vulnerable: VU B1 a,b(i,ii,iii,iv) according to IUCN (2014) guidelines. The multiple threats listed above, and our alternative EOO and AOO, indicate that a future conservation status of Endangered for *K. celebica* may be appropriate when further data become available.

The rediscovery of little-known legume genera continues to shed light on previously unresolved relationships within the legume family (Cardoso et al. 2017). Combined morphological and phylogenetic data places *Kalappia* in a Southeast Asian/Pacific/Australian clade alongside the genera *Storckiella, Petalostylis* and *Labichea* (Zimmerman et al. 2017). *Storckiella* inhabits wet tropical areas of New Caledonia, Australia and Fiji, while *Petalostylis* and *Labichea* grow in arid regions of Australia (Lewis 2005). Coupled with this biogeographic distinction is an association of all the four genera to phytonutrient poor, heavy

metal rich, ophiolitic soils (ultramafic soils being a high nickel concentration example, formed over mantle-derived geology).

Phylogenetic biome conservatism is the phenomenon whereby plant lineages are generally confined to a particular biome (Pennington and Lavin 2016). From a plant trait perspective, biome conservatism is intuitive, due to successful biome inhabitation permitting a high likelihood that the lineage's trait complement is advantageous for colonisation of similar bioclimatic regions. There are, however, clades and specific landscapes that offer contrasting distribution patterns (Cardillo et al. 2017). This is the case for the *Kalappia, Storckiella, Petalostylis* and *Labichea* clade that exhibits edaphic conservatism (found on ophiolitic soils) but heterogeneity in biome (tropical and arid). Added to this, these genera have a pan Austral-Asian distribution occupying mainland Australia and islands from Sulawesi to Fiji. This clade, therefore, has the potential to provide empirical evidence for the dual impact of environmental variability and an archipelagic setting upon dispersal. This may help us understand the environmental variables that underpin the segregation of the flora into the regions of Sunda, Wallacea and Sahul (van Welzen et al. 2011).

Generic gaps still remain in the legume phylogeny. Within subfamily Dialioideae, in which *Kalappia* is placed, the genera *Uittienia* and *Androcalymma* are yet to be sampled (Zimmerman et al. 2017) and, like *Kalappia* previously, recent collections are lacking. Their modern collection and conservation status assessment remain a priority.

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